The Population Dynamics and Conservation of the African Black Oystercatcher *Haematopus moquini*

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For my father – who has given so generously of his humour, his wisdom and his encouragement and has always "...bent my spirit up to its true height...".

Declaration

I hereby declare that the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

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Douglas Loewenthal Date

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The nature of this project was such that it would never have been possible without a considerable collective effort.

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GENERAL ABSTRACT

The African Black Oystercatcher is currently classified as *Near-threatened* by virtue of the fact that the population size is small (<10 000) and numbers have decreased or were previously recorded as decreasing. Aspects considered to be of conservation concern to the species are (a) its inherently low and variable breeding success; (b) its ground-nesting habit, making it vulnerable to numerous direct and indirect impacts of human disturbance; (c) its susceptibility to mass mortalities, particularly of adult birds in high-density breeding populations. Inherent factors which may of benefit to the species' persistence are its considerable longevity and, potentially, a degree of connectivity between local populations, although current evidence suggests that this is very low. However, in addition to these considerations, over the past 25+ years the variety and intensity of potential threats and benefits to the species have also changed and this may have changed the species' conservation status. While human activity has increased in many areas of the species' breeding range, African Black Oystercatcher populations may be benefiting from and increase in the number of Marine Protected Areas as well as an improved food supply in the form of an invasive alien mussel species, *Mytilus galloprovincialis*. In light of the key factors outlined above and the territorial nature of the species, all of which are considered to be of importance to the species' population dynamics and conservation, the main aims of this study were to: (a) reassess the global population and, where changes have occurred, to provide an explanation for these changes; (b) assess the importance of, and manner in which human disturbance may impact breeding populations; (c) assess levels of natal site philopatry and adult site fidelity in local populations; (d) assess the long-term population viability of the species; and (e) assess the potential importance of territorial behaviour in governing the population dynamics of local oystercatcher populations. The study demonstrated that the global population has increased over the past 25 years, from *ca* 5000 birds to *ca* 6670 birds and that both the presence of *Mytilus galloprovincialis* and improved protection have benefited the

species. Despite an increase in the global African Black Oystercatcher population, a number of local populations have experienced decreases in numbers. Most of these decreases appear to be as a result of localised movement of birds out of areas which have experienced human-induced habitat degradation, rather than because of unsustainable reproductive rates *per se*. Nevertheless, for several unprotected local oystercatcher populations breeding success was below the minimum required to maintain a stable population (*ca* 0.28 fledglings.pair^{-1}.year^{-1}). In unprotected areas, uncontrolled dogs depredating chicks, and the drowning of chicks hiding from humans and their associated pets, appear to be the most important ways in which human activity is impacting the breeding success of African Black Oystercatchers. This study demonstrated very high levels of natal philopatry and adult site fidelity for the species, suggesting little widespread connectivity between oystercatcher populations. Despite the low potential for large-scale, source-sink dynamics, long-term population viability analyses demonstrated a very low risk of population extinction at a global or regional scale, even under unrealistically adverse conditions. Although improved reproductive success is likely to explain the global population increase, local increases in breeding numbers appear to be largely as a result of territory shrinkage of existing breeding pairs in response to improved habitat quality, with a resultant influx of previously excluded, sexually mature birds. The study further suggests that the long-term carrying capacity of local, breeding African Black Oystercatcher populations is determined almost entirely by resource availability, rather than competitor density. Overall, the results from this study suggest that there has undoubtedly been a considerable improvement in the species' conservation status over the past two decades, partly as a result of improved coastal conservation measures and partly as a result of increased food supply. Given current trends it may well be possible in the near future to propose the species' removal from the IUCN Red List.

CHAPTER 1

GENERAL INTRODUCTION

The African Black Oystercatcher, *Haematopus moquini*, like some of the world's other oystercatcher species, exhibits a suite of characteristics which, together with extrinsic factors, make its conservation status a potential cause for concern.

In the first instance it is a highly range-restricted species with a relatively small population size, even amongst the Haematopodidae. It has been estimated that approximately 75% of the global African Black Oystercatcher population is restricted to the South African mainland coast and associated offshore islands and it is the third rarest as well as one of the most range-restricted oystercatcher species (Hockey 1983a). Unlike the Eurasian Oystercatcher *H. ostralegus*. which has successfully colonised inland habitats (Goss-Custard *et al.* 1996), the African Black Oystercatcher is an exclusively coastal species and breeding adults, non-breeding mature birds and immature birds must all satisfy their varying needs primarily within the coastal zone (Hockey 1983a, Leseberg 2001, Rao 2005). During the late 1970s and early 1980s a near-complete survey estimated the global population size at *ca* 5000 birds, with probably no more than 2000 breeding pairs (Hockey 1983a).

While island populations of African Black Oystercatchers form a significant proportion of the global population, the majority of the population occurs on the mainland (Hockey 1983a), with a breeding range extending from about Lüderitz (26°38'S, 15°10'E), southern Namibia, to Port Edward (31°03'S, 30°14'E) on the southern Kwazulu/Natal coast (Hockey *et al.* 2003) (Fig 1.1). In the late 1970s, introduced mammalian predators were identified as a major threat to island populations (Summers & Cooper 1977), and, given the importance of islands (particularly on the west coast of South Africa) for breeding oystercatchers, improved protection of these sites was motivated (Hockey 1983a) and, in some cases, actioned. Currently, the majority of islands with important breeding populations of oystercatchers receive a high level of protection (Lombard *et al.* 2004) and current impacts on these populations are likely to be restricted to natural phenomena. In

particular, mass mortalities of oystercatchers due to Paralytic Shellfish Poisoning (PSP) may be of particular importance to the dynamics of oystercatcher populations on islands off the west coast of South Africa. In one instance the impact, even at a population level was severe, with five high-density island populations being approximately halved during the outbreak (Hockey and Cooper 1980)

With some exceptions, island populations of African Black Oystercatchers are characterised by having a relatively high breeding success – not only due to protection, but also due to a lack of terrestrial predators. There is some evidence that these island populations are producing surplus birds (Hockey & Cooper 1980) and it has been suggested that chick production on predator-free offshore islands may be crucial for maintaining the mainland breeding population (Hockey 1996a). In general, permanent movement of juveniles (or adults) away from natal sites to other areas may increase connectivity between local populations and improve the status of otherwise isolated populations (Root 1998, Saether *et al.* 2005). Thus, an understanding of the phenomena of site fidelity and natal philopatry are of potential importance for a species' conservation. Some species within the Haematopodidae do display high levels of natal philopatry (Hockey 1996a), and adult African Black Oystercatchers display very high site tenacity (Hockey 1983a). However, little is known about the degree of natal philopatry in African Black Oystercatchers, although there is some evidence for a high return rate of juvenile birds to natal breeding grounds (Hockey 1983a,b). In general, high site fidelity of adult birds, together with the formation of long-term pair bonds that are characteristic of most and possibly all oystercatcher species, creates the potential for high levels of natal philopatry (Hockey 1996b) and there is ample evidence that this is the case for Eurasian Oystercatchers (Ens *et al.* 1996).

Both theoretical (Ens *et al.* 1995) and empirical studies (Heg 1999, Heg *et al.* 2000, Bruinzeel & Pol 2004) of Eurasian Oystercatchers suggest that levels of natal philopatry and age-at-first breeding are interrelated and are based on the life-history decisions of potential breeders. These phenomena are all important considerations in explaining population dynamics (Lack 1967, Burger and Gochfeld 1986, Hanski 2001) and have important conservation implications (Root 1998, Heppel & Crowder 1998, Heppel *et al.* 2000, Saether and Bakke 2000, Saether *et al.* 2005). While movement patterns of young African Black Oystercatchers of three years old and less are now fairly well understood (Hockey *et al.* 2003, Rao 2005), virtually nothing is

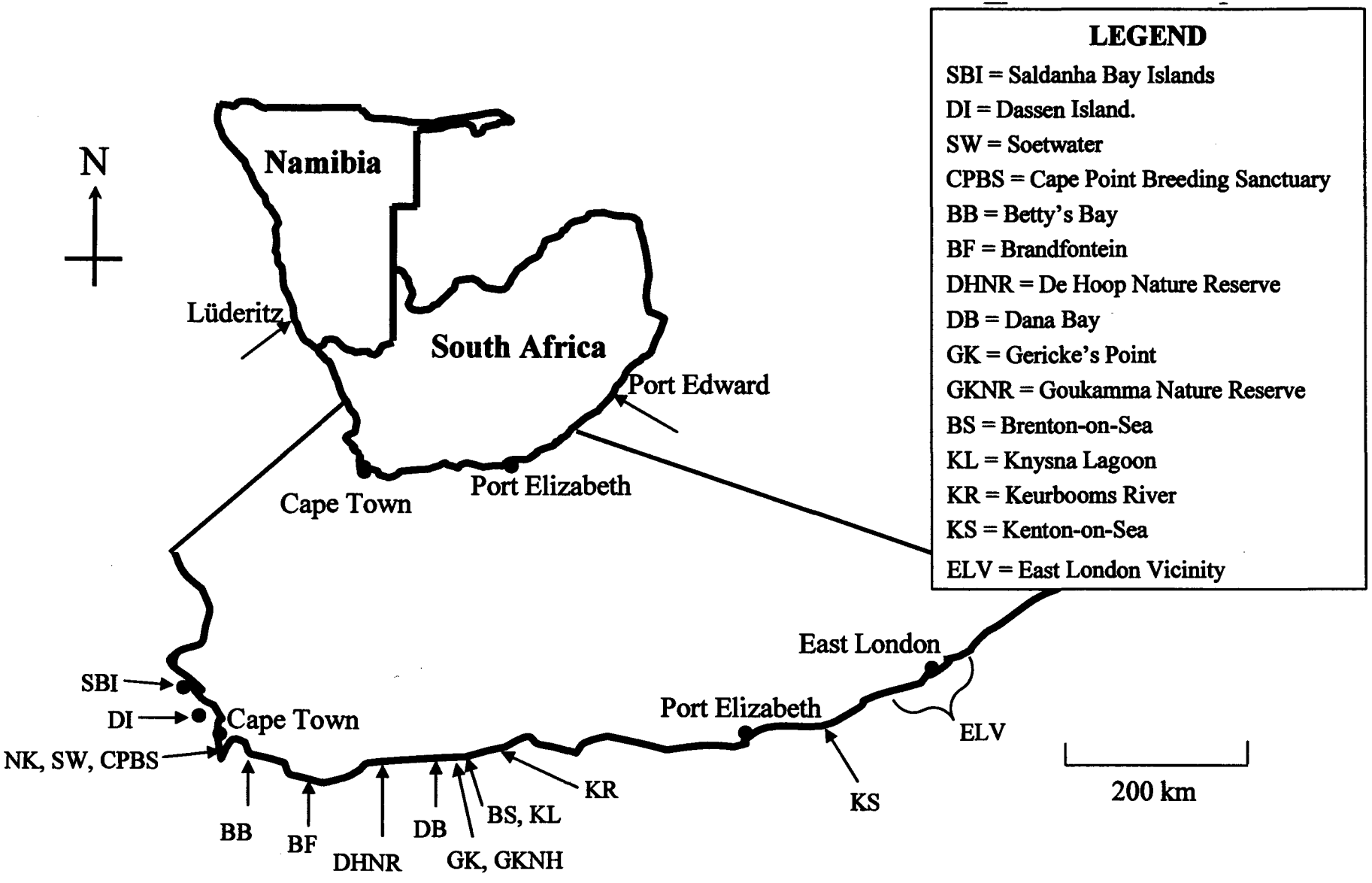

Fig. 1.1. Map of southern Africa (inset) and enlarged section of the South African coast indicating the location of field sites which formed the foci of the study. Arrows on the inset map indicate the current limits of the breeding range of African Black Oystercatchers on the mainland of southern Africa.

known of the biology of African Black Oystercatchers potentially able to breed, but which have not yet become established as breeders (i.e. 'floaters'). Although populations of African Black Oystercatchers on islands are currently well protected, potentially high levels of natal site philopatry and adult site fidelity may mean that ailing mainland populations (that are generally not well protected) are not supplemented by surplus birds from island populations or from other mainland populations (such as those in high-quality habitats with high levels of protection).

On the mainland coast of South Africa, several factors, both intrinsic and extrinsic, have made the oystercatcher's status a cause for conservation concern since the 1980s. Birds breed on the open coast during the austral summer (November - March), at the height of the holiday season (Hockey 1983b). Clutch sizes are small, ranging from one to (rarely) three, with a modal size of two (Hockey 1983b). Young birds become sexually mature at three (females) to four (males) years (Hockey 1996a), but most are likely to acquire a breeding territory only after 5 or more years (Loewenthal 1998). Thus, oystercatchers have a slow turnover rate and may not be able to recover rapidly from periods of low breeding success or high adult mortality. On Marcus Island (33°02'S, 17°58'E) in Saldanha Bay, a causeway linking the island to the mainland was completed in 1976. This allowed mammalian predators access to the island and, despite a predator-proof barrier being erected in 1981 (Hockey 1983a), the population has virtually halved over the past 20 years (since 1996 numbers have remained stable at around 60 individuals, but there has been no sign of recovery).

Because of the siting and timing of their breeding attempts, African Black Oystercatchers are vulnerable to the direct and indirect effects of human disturbance (Jeffery 1987, Hockey 1996b). As a result, their breeding success (fledglings per pair per year) outside protected areas may be lower than within protected areas on the mainland. Human disturbance and exploitation of intertidal invertebrates are thought to have been the key factors responsible for the extinction of the Canarian Black Oystercatcher *H. meadewaldoi* (Hockey 1987). Direct effects of human disturbance have been identified as destruction of nests by walkers and off-road vehicles (ORVs) and predation of chicks by uncontrolled dogs (Jeffery 1987, Hockey & Loewenthal 2002). Potential indirect effects of human disturbance include death of unattended eggs and small chicks through heat exposure (Webb 1987, Adams *et al.* 1999). Disturbance may also result in drowning of chicks (pers. obs.) and loss of adult foraging time (Lambeck *et al.* 1996), possibly leading to chick starvation.

Chick starvation in the face of human disturbance may be of particular importance because oystercatchers have an expensive mode of chick provisioning involving single-prey loading and mobile Central Place Foraging, a strategy that has been defined as 'precocial 5' (Safriel *et al.* 1996). The foraging of adults is tidally constrained (Hockey and Underhill 1984) and, due to the complex techniques involved in learning how to forage, adults are entirely responsible for chick provisioning until well after chicks have fledged (Hockey 1981, 1996b). Furthermore, it has been widely demonstrated that human disturbance can significantly reduce the foraging success of adult oystercatchers (Lambeck *et al.* 1996, FitzPatrick & Bouchez 1998, Coleman *et al.* 2003) and, in the case of the Eurasian Oystercatcher, that experimentally increasing human disturbance of breeding birds reduces the proportion of food allocated to chicks (Verhulst *et al.* 2001). Because there is a gradient of decreasing intertidal productivity on South Africa's rocky shores from the Atlantic Ocean coast in the west to the Indian Ocean coast in the south and east (Bustamante *et al.* 1995), the severity of this potential human impact is likely to vary geographically. A simple time-energy budget model suggests that even in many undisturbed areas, parent birds may struggle to rear two or even one offspring up to fledging and that these energetic constraints increase with decreasing intertidal productivity (Leseberg *et al.* 2000).

Disturbance levels are likely to continue to increase, as the number of people using the South African coast has increased markedly in recent years (e.g. Watson & Kerley 1995, Prochazka & Kruger 2001), as has the coastal population: for example, the human population around Table Bay (the port of Cape Town) rose from 301 500 in 1936 to 827 000 in 2001 (Statistics South Africa 2005).

Despite the potential threats facing African Black Oystercatchers, a number of measures have been implemented on the mainland to conserve the species, including increased reserve proclamation in recent years (Lombard *et al.* 2004), and, since 2000, a nationwide off-road vehicle ban on South African beaches (Department of Environmental Affairs and Tourism 2003, 2004), although no equivalent ban exists in Namibia. Increased reserve proclamation is already known to have significantly benefited some oystercatcher populations (e.g. Leseberg *et al.* 2000), and there is some evidence that the off-road vehicle ban has improved the breeding success of oystercatchers (Williams *et al.* 2004).

In addition to increased protection, there is another factor which may well be benefiting oystercatcher populations on the mainland coast of South Africa, namely an increased food supply in the form of an alien invasive Mediterranean mussel, *Mytilus galloprovincialis* (Robinson 2005, Robinson *et al.* 2005, Wieters 2006). *Mytilus* was first recorded in Saldanha Bay in the mid-1970s and in 1990, it was translocated from the west coast to Port Elizabeth (33°40'S, 25°40'E) on the south coast, for myticulture (Branch & Steffani 2004). From Port Elizabeth it has subsequently spread both east and west and is now well established along the coastline between Swakopmund, Namibia (22°40'S, 14° 32'E) and Kidd's Beach, Eastern Cape (32°40'S, 28°25'E): in terms of biomass, it is now the dominant intertidal bivalve on the west coast of South Africa (Branch & Steffani 2004). There is good evidence to link the subsequent invasion of *Mytilus* to an increase in the population of oystercatchers on islands in Saldanha Bay. On Jutten (33°05'S, 17°57'E) and Malgas (33°03'S, 17°56'E) Islands, the proportion of *Mytilus* in the hard-shelled diet of oystercatchers increased between the early 1980s (when it was introduced) and the early 1990s. Concomitant with this shift in diet, oystercatcher productivity (measured as the ratio of two- to one-chick broods) also increased (Hockey & Van Erkom Schurink 1992).

While changes in habitat quality (such as changes in food supply and human disturbance) may influence the productivity of oystercatcher populations, behavioural responses to changes in habitat quality may also be important in explaining oystercatcher population dynamics and may have significant conservation implications. Oystercatchers are conspicuous by their territorial behaviour and territorial exclusion of sexually mature birds may be an important form of population regulation if the number of adults excluded from territories is large (Harris 1970, Ens 1992, Goss-Custard *et al.* 1995, Newton 1998, Heg 1999). Characteristics of populations regulated by territorial exclusion typically include rapid replacement of removed territorial pairs and the presence of large numbers of birds near or adjacent to either prime breeding and/or feeding habitat (Newton 1998). In 1978, an outbreak of Paralytic Shellfish Poisoning (PSP) virtually halved oystercatcher populations on five islands off South Africa's west coast (Hockey & Cooper 1980), but these losses were replaced rapidly: one year later, populations were already at approximately 80% of pre-PSP levels (Hockey & Cooper 1980). Similarly, in 1999, populations on Malgas and Jutten Islands were reduced by approximately 30%, but numbers

recovered in less than one year (D. Loewenthal unpubl. data). These are replacement rates that cannot be explained by intrinsic growth. The presence of large numbers of surplus birds attempting to acquire territories, but prevented from doing so, means that breeding populations comprising territorial individuals typically are tightly regulated, with some fluctuation from year to year, but with little real change in numbers, unless there is a change in habitat quality (Krebs 1970, Patterson 1980). Ultimately, understanding how characteristics of the environment (e.g. food abundance), of behaviour (e.g. territoriality) and of populations (e.g. densities) interact is essential in understanding, for example, how populations respond to changes in habitat quality (Patterson 1980). The possible population consequences of habitat loss for European Oystercatchers have already been well studied, both at local and continental scales (e.g. Sutherland & Dolman 1994, Dolman & Sutherland 1995, Goss-Custard *et al.* 1996, Durell *et al.* 1997), but little is known about how African Black Oystercatcher populations may respond to habitat loss or degradation, even at a local scale. Such insights, however, cannot be gained without some understanding of the way in which population and environmental variables are interlinked.

The regional Red Data Book (Barnes 2000) classifies the African Black Oystercatcher as *Near-threatened* by virtue of the fact that the population size is small (<10 000) and numbers have decreased or were previously recorded as decreasing. However, over the past 25+ years the variety and intensity of potential threats and benefits to the species have changed and this may have changed the conservation status of the species. In light of the key factors outlined above, which are considered to be of importance to the species' population dynamics and conservation, the main aims of this study were to:

1. Reassess the global African Black Oystercatcher population and, where changes have occurred, to assess the reasons for these changes, with particular focus on the possible importance of *Mytilus galloprovincialis* and protection status for the species (Chapter 2).

2. Assess the relative importance of *Mytilus galloprovincialis* and protection status on the breeding success of oystercatchers and to investigate how and to what extent human disturbance may be acting to influence the breeding success of local populations (Chapter 3).

3. Investigate the possibility of chick starvation as a potentially important form of human induced mortality and assess whether the presence of *Mytilus galloprovincialis* may ameliorate such energetic stress (Chapter 4).

4. Assess levels of natal site philopatry and adult site fidelity for the species and investigate what factors influence the pattern of recruitment of first-time-breeders into the population (Chapter 5).

5. Assess the population viability of the species with key regard to variability in breeding success, variability of adult mortality rates (particularly episodic mass mortalities), recruitment pattern of non-breeding birds into the breeding population, and connectivity between populations (Chapter 6).

6. Investigate the interaction between territorial breeding birds and nonbreeding birds on the population dynamics of the species, with key regard to how this might influence the response of local populations to changes in habitat quality, local population viability and the long-term carrying capacity of local breeding populations (Chapter 7).

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CHAPTER 2

AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI* POPULATION TRENDS: CAUSES AND CONSEQUENCES

INTRODUCTION

The African Black Oystercatcher *Haematopus moquini* is an exclusively coastal species with a breeding range extending from about Lüderitz (26°38'S, 15°10'E), southern Namibia, to the Inhlanhlani River mouth near Port Edward (31°03'S, 30°14'E) on the southern Kwazulu/Natal coast (Brown & Hockey 2007) (Fig. 1.1).

During the late 1970s and early 1980s a near-complete survey of the Namibian and South African coast estimated the global population size at *ca* 5000 birds, with probably no more than 2000 breeding pairs (Hockey 1983a). Approximately 75% of the global population is restricted to the South African coast and it is the third rarest, as well as one of the most range-restricted of the Haematopodidae: it is currently classified as *Near-threatened* both in South Africa and globally (Barnes 2000, Birdlife International 2004), and is listed as a 'specially protected vertebrate' in Namibia (R. Simmons *in litt.*). In the late 1970s, introduced mammalian predators were identified as a major threat to island populations (Summers & Cooper 1977), and, given the importance of islands (particularly on the west coast of South Africa) for breeding oystercatchers, improved protection of these sites was motivated (Hockey 1983a) and, in some cases, actioned.

On the mainland coast of South Africa, several other factors, both intrinsic and extrinsic, have made the oystercatcher's status a cause for conservation concern since the 1980s. Birds breed on the open coast during the austral summer (November - March), at the height of the holiday season (Hockey 1983b). Clutch sizes are small, ranging from one to (rarely) three, with a modal size of two (Hockey 1983b). Young birds become sexually mature at three (females) to four (males) years (Hockey 1996a), but most are likely to acquire a breeding territory only after 5 or more years (Loewenthal 1998). Thus, oystercatchers have a slow turnover rate and are unlikely to be able to recover rapidly from periods of low breeding success or high adult

mortality (although a floater population may buffer the impacts of short, but severe periods of high adult mortality occasioned by disease or biotoxins (Ch. 6)). On Marcus Island (33°02'S, 17°58'E) in Saldanha Bay, a causeway linking the island to the mainland was completed in 1976, allowing mammalian predators access to the island. A predator-proof barrier was erected in 1981 (Hockey 1983a), but its design was ineffective and the population halved in the following 15 years. Since 1996 numbers have remained stable at around 60 individuals, but there has been no sign of recovery.

Because of the siting and timing of their breeding attempts, African Black Oystercatchers are vulnerable to the direct and indirect effects of human disturbance (Jeffery 1987, Hockey 1996b); for example, human disturbance and exploitation of intertidal invertebrates are thought to have been the key factors responsible for the extinction of the Canarian Black Oystercatcher *H. meadewaldoi* (Hockey 1987). Among African Black Oystercatchers, breeding success (fledglings.pair^{-1}.year^{-1}) outside protected areas is lower than in protected areas (Ch. 3). Direct effects of human disturbance have been identified as destruction of nests by walkers and off-road vehicles (ORVs) and predation of chicks by uncontrolled dogs (Jeffery 1987, Hockey & Loewenthal 2002). Potential indirect effects of human disturbance include death of unattended eggs and small chicks through heat exposure (Webb 1987, Adams *et al.* 1999). Disturbance may also result in drowning of chicks (pers. obs.) and loss of adult foraging time (Lambeck *et al.* 1996), possibly leading to chick starvation (although this probably occurs rarely – Ch. 4). Disturbance levels are likely to continue to increase, because the number of people using the South African coast has increased markedly in recent years (e.g. Watson & Kerley 1995, Prochazka & Kruger 2001), as has the coastal population: for example, the human population around Table Bay (the port of Cape Town) rose from 301 500 in 1936 to 827 000 in 2001 (Statistics South Africa 2005).

Measures have been implemented on the mainland to conserve the species, including increased reserve proclamation over recent years (Lombard *et al.* 2004), and, since 2000, a nationwide off-road vehicle (ORV) ban on South African beaches (Department of Environmental Affairs and Tourism 2003, 2004), although no equivalent ban exists in Namibia. Reserve proclamation has significantly benefited oystercatcher populations (Leseberg *et al.* 2000), and there is already some evidence that the ORV ban has improved the breeding success of oystercatchers (Williams *et*

al. 2004), although changes in breeding numbers appear to have been due mostly to increased settlement of birds in the study areas rather than intrinsic recruitment (Ch. 7). However, there is another factor, besides protection, which may well be benefiting oystercatcher populations on the mainland coast of South Africa: namely an increased food supply in the form of an alien invasive mussel, *Mytilus galloprovincialis* (Robinson 2005, Robinson *et al.* 2005, Wieters 2006). *Mytilus* was first recorded in Saldanha Bay in the mid-1970s, although final confirmation of the species' identity and its site of introduction were only obtained in 1985 (Grant & Cherry 1985). There is good evidence to link the subsequent invasion of *Mytilus* to an increase in the population of oystercatchers on islands in Saldanha Bay. On Jutten (33°05'S, 17°57'E) and Malgas (33°03'S, 17°56'E) Islands, the proportion of *Mytilus* in the hard-shelled diet of oystercatchers increased between the early 1980s (when it was introduced) and the early 1990s. Concomitant with this shift in diet, oystercatcher productivity (measured as the ratio of two- to one-chick broods) also increased significantly (Hockey & Van Erkom Schurink 1992).

Subsequent to its invasion of Saldanha Bay, *Mytilus* spread rapidly and became the dominant mussel species along the Cape west coast (Griffiths *et al.* 1992, Hockey & Van Erkom Schurink 1992). In 1990, it was translocated from the west coast to Port Elizabeth (33°40'S, 25°40'E) on the south coast for myticulture (Branch & Steffani 2004). From Port Elizabeth it has subsequently spread both east and west and is now well established along the coastline between Swakopmund, Namibia (22°40'S, 14° 32'E) and Kidd's Beach, Eastern Cape (32°40'S, 28°25'E), with no further range expansion reported since 2000 (Robinson 2005). It is now the dominant intertidal bivalve on the west coast of South Africa (Branch & Steffani 2004). *Mytilus* occurs intertidally and out competes the limpet *Scutellastra granularis* and the indigenous Ribbed Mussel *Aulacomya ater* for space due to higher desiccation tolerance, faster growth rates and greater fecundity (Griffiths *et al.* 1992, Hockey & Van Erkom Schurink 1992). Additionally, it is not infected by the trematode parasites that are common in indigenous mussels and which reduce both individual growth rates and reproductive output (Calvo-Ugarteburu & McQuaid 1998a, 1998b). *Mytilus* not only displaces the indigenous mussels and limpets, but also reaches higher densities and biomass than the species it has replaced (Griffiths *et al.* 1992, Robinson *et al.* 2005) and occurs higher up in the intertidal zone than the native *Aulacomya ater*

(Van Erkom Schurink & Griffiths 1990), making it potentially available to oystercatchers for a longer period of the tidal cycle.

Whatever the cause of oystercatcher population changes, several lines of evidence suggest that widespread local increases, and hence possibly a global increase in oystercatcher numbers has occurred since the early 1980s. Besides increases already mentioned, numbers of oystercatchers between the Maitland (33°59'S, 25°17'E) and Gamtoos (33°58'S, 25°10'E) River estuaries increased from 70 birds in 1970 to 212 in 1994 (Hockey 1983a, Watson & Kerley 1995) and at Cape Recife, Port Elizabeth (an area with considerable recreational disturbance) there was an increase in numbers from three birds in 1983 to 23 by 1988 (Spearpoint *et al.* 1988). At the eastern extremity of the breeding range (in the vicinity of East London) numbers trebled between 1983 and 2004 (Vernon 2004) and there has also been a considerable eastward expansion of the breeding range from Mazeppa Bay in 1983 (Hockey 1983a) 240 km east to the Inhlanhlani River mouth near Port Edward, southern Kwazulu/Natal (Brown & Hockey 2007). Although not yet recorded breeding east of southern KwaZulu-Natal, the species' frequency of occurrence in central and northern KwaZulu-Natal has increased rapidly in recent years (Brown & Hockey 2007).

In light of these local population changes and the putative factors driving them, this study had two major aims: (1) To reassess the global African Black Oystercatcher population; (2) to assess the relative influence of the *Mytilus* invasion and protection measures on oystercatcher populations.

METHODS

Population trends and current population estimates

To investigate population trends in oystercatcher numbers and to reassess the global population size, several data sources were utilised.

Historical survey data

Complete coastal counts (on sections of coastline of known length and habitat type) of adult oystercatchers (>1 yr old) were undertaken during the late 1970s and early 1980s between the Kunene River (at the Namibia/Angola border) and the Kei River (South Africa) (Underhill & Cooper 1982). Counts east of the Kei River and

extending to Coffee Bay (31°29'S, 29° 13'E), as well as historical count data from offshore islands around the South African coast were also available (Hockey 1983a).

Recent Survey Data

Mainland coast: Namibia and the Northern Cape: Aerial surveys were made of the entire coastline between the Olifants River (31°40'S, 18°10'E) and Lüderitz (26°38'S, 15°10'E) during 4-7 May 2004, and from Lüderitz to the Kunene River (17°52'S, 12°10'E) during 28-30 August 2004. Surveys were conducted during the high-tide period and numbers at roosts along the coast were counted. It was assumed that birds breeding on islands off the coast of Namibia do not join mainland birds at high tide roosts. Aerial surveys did not include known aggregations of birds at Walvis Bay (22°57'S, 14°32'E) and Swakopmund (22°40'S, 14°32'E): at these sites, average summer and winter counts were obtained from Wearne & Underhill (2005) and Leseberg (2001) respectively.

South Africa: Western and Southern Cape: As part of the Oystercatcher Conservation Programme (OCP), surveys were carried out on an annual basis between 1997 and 2002 along the South African coastline between the Olifants River and the Kei River (although these surveys did not cover the entire coastline). The precise locations of all birds were recorded on 1:50 000 topographical maps, allowing for direct comparison of recent and historical counts for extensive stretches of the South African coastline. All adult (>1yr old) African Black Oystercatchers were counted, and counts were made on a falling tide as far as possible, to minimize tidally influenced movement and maximise accuracy of feeding habitat preference.

Former Transkei: Oystercatchers in the former Transkei were counted during November/December 2000 between the Kei River and Ramsgate (31°03'S, 30°14'E), southern Kwazulu/Natal (N. Smith *in litt.*).

Namibian Islands: Average summer counts were obtained from 1993, 1995 and 2003 for the following Namibian islands: Staple Rocks (26°21'S, 14°59'E), Dumfudgeon Rocks (26°30'S, 15°07'E), Seal (26°36'S, 15°10'E), Shark (26° 38'S, 15° 09'E), North Long (26°49'S, 15° 07'E), Lady's Rocks (26°51'S, 15°09'E), Albatross Rocks (27°07'S, 15°14'E), Penguin (26° 37'S, 15°10'E), Pomona (27°11'S, 15°15'E) and

Sinclair (27° 40'S, 15°31'E) (Marine and Coastal Management unpubl. data). For Possession Island (27°01'S, 15°12'E) and Ichaboe Island (26°17'S, 14°56'E) counts were obtained from Namibian Fisheries (unpubl. data). These were summer averages for 2004 and 2005, and between 1998 & 2004, for the two islands respectively. Counts for Mercury (25° 43'S, 14° 50'E), Flamingo (26°35'S, 15°10'E) and Halifax (26°39'S 15°05'E) were obtained from Simmons *et al.* (unpubl. data).

South African Islands: Counts from Bird Island (Lambert's Bay) (32°05'S, 18°18'E) were obtained for the period 1997-2002, and were averaged (V. Ward *in litt.*). Counts from 1999 and 2001 were available for Schaapen (33°05'S, 18°02'E) and Meeuw Islands (33°05'S, 18°01'E) (Marine and Coastal Management unpubl. data). Malgas (33°03'S 17° 56'E), Jutten (33°05'S, 17°58'E) and Marcus (33°03'S, 17°58'E) Islands were all counted at least twice each summer between 1998 and 2005, and an average value was calculated for each island. The population on Vondeling (33°09'S, 17°59'E) was estimated by calculating the mean proportional change in oystercatcher population size on Malgas and Jutten and applying it to the population estimate from 1979/1980 for Vondeling. Due to the proximity of these three islands, and their similar protection status (Hockey 1983a) it was assumed that trends would be similar (as they have been for Malgas and Jutten – Fig. 2.2). Summer counts for Dassen Island (33°26'S, 18°05'E) were obtained for 2002, 2003 and 2004 (J. Visagie *in litt.*) and were averaged. Data for Robben Island (33°49'S, 18°22'E) were extracted from Calf & Underhill (2002). Count data for Dyer Island (34°41'S, 19°25'E) were obtained for 1998 and 2002 and a mean was calculated (Marine and Coastal Management unpubl.data). No recent data were available for Seal Island (False Bay) (34°08'S, 18°07'E) or Geyser Island (34°41'S, 19°25'E) and they were omitted from the analysis: it is unlikely that there are permanent populations on either of these islands - historically, they were simply recorded as 'present' on Seal and only one bird was ever observed on Geyser (Hockey 1983a). Seal Island (Mossel Bay) (34°09'S, 22°07'E) and St. Croix Island (33°48'S, 25°46'E) were counted in August 1996 and the Bird Island group (33°50'S, 26° 17'E) in Algoa Bay was surveyed each summer between 1997 and 2004 (N. Klages *in litt.*).

Coastal Wetlands: The mean numbers of oystercatchers counted at coastal wetlands between 1992 and 1997 were obtained from Taylor *et al.* (1999).

Coastline Divisions

For the purpose of analyses, and to allow for comparisons between historical and recent survey data, the southern African coastline was divided in three different ways, with resultant stretches of coast being defined as *Regions*, *Sub-Regions* or *Sections* (which were further subdivided according to shore type). The latter, defined stretches of coast are different in length and allowed for changes in oystercatcher population numbers to be analysed at different scales. The *Regions* and *Sections* used in this study were the same as those used by Hockey (1983a) to estimate the global population, thus allowing for direct and simple comparison between previous and current population estimates.

Regions: The southern African coastline, covering the current breeding range of adult African Black Oystercatchers, was divided into five *Regions* (after Hockey 1983a): (1) Kunene River to the Orange River (28°37'S, 16°28'E); (2) Orange River to the Olifants River; (3) Olifants River to Mossel Bay (34°09'S, 22°07'E); (4) Mossel Bay to the Kei River; and (5) Kei River to Ramsgate. [Note: The eastern boundary of surveys in the former Transkei extended to Coffee Bay in the 1980 survey and to 3 km south of Ramsgate in the 2000 survey. Although there is a discrepancy in distance, the breeding range is known to have expanded 240 km eastwards (Nevill 1999) since the early 1980s (Hockey 1983a)].

Sub-regions: The coastline was divided into *Sub-regions* at a finer scale than the *Regions*. Only sites where counts were made during both the historical and the recent surveys (1997-2002) were included. These were: (1) Kunene River to the Orange River; (2) Orange river to the Olifants River; (3) Olifants River to Cape Point (34°20'S, 18°30'E); (4) Cape Point to Mossel Bay; (5) Mossel Bay to Port Elizabeth (33°40'S, 25°40'E); (6) Port Elizabeth to the Kei River; and (7) The Kei River to Ramsgate. *Sub-regions* 3-6 included both historical and recent site-specific counts. Thus these areas could be, and were compared statistically (Wilcoxon matched-pairs tests).

Sections: The South African coastline between the Olifants river and the Kei River was divided into *ca* 200 km *Sections*: (1) Olifants River to Slipper Bay (32° 46' S 18°01'E); (2) Slipper Bay to Cape Point; (3) Cape Point to Cape Agulhas (34°48'S,

20°02'E); (4) Cape Agulhas to Mossel Bay; (5) Mossel Bay to Tsitsikamma (34°05'S, 23°45'E); (6) Tsitsikamma to Port Elizabeth; (7) Port Elizabeth to Cape Padrone (33°40'S, 26°35'E); and (8) Cape Padrone to the Kei River. Within these *Sections*, three shore types were identified, namely sandy, rocky and mixed shores. Rocky or sandy shores were defined as stretches of coast of at least 200 m of either rock or sand, with mixed shores being stretches of at least 200 m of interdigitated rock and sand. These divisions were used as a basis to compare changes in oystercatcher number by habitat type within each 200 km *Section*.

For each site that was surveyed both historically and recently, the proportional change in oystercatcher population size was calculated. Proportional changes by habitat type were averaged to obtain an extrapolation factor which was applied to historical counts to estimate current population numbers for stretches of coast not surveyed between 1997 and 2002 within the same *Section* and on the same shore type. An extrapolation factor was calculated for each shore type within each *Section*, and the process repeated for all eight *Sections*. An error estimate for these extrapolations was calculated as ± 2 S.D. from the mean estimated number of oystercatchers per site. The minimum, mean and maximum population size estimate per site were pooled to obtain minimum, maximum and mean size estimates for each *Section* by shore type. In instances where no birds were counted at sites in the historical survey and birds were present in the recent survey, no attempt was made to calculate a proportional size change. For sites where no birds were recorded during historical surveys and which were not re-surveyed recently, it was conservatively assumed that there were still no birds.

The influence of *Mytilus* and protection on oystercatcher population trends

To assess the possible influences of *Mytilus* and protection on oystercatcher population numbers, two approaches were taken.

Year of Mytilus *invasion and population-wide trends*

A population-wide assessment of the influence of *Mytilus* on oystercatcher numbers was made by comparing the year of invasion of *Mytilus* with (a) proportional changes in oystercatcher population size, (b) changes in population density, and (c) absolute changes in population size, at a number of sites on both mixed and rocky shores throughout the breeding range. Changes in the latter three parameters were established

by comparing historical counts with recent survey data. Although *Mytilus* has recently been recorded invading sandy shore habitats (Robinson & Griffiths 2002), it is predominantly a rocky-shore invasive (Hockey & Van Erkom Schurink 1992). Restricting analyses to either rocky or mixed shores where recent and historical survey data existed (i.e. between the Olifants and Kei Rivers) resulted in a total of 98 sites where population changes could be assessed in relation to the timing of *Mytilus* invasion. Data on the year of *Mytilus* invasion at 16 localities between Swakopmund and East London were obtained from Robinson (2005). Because most sites (where changes in oystercatcher numbers were established) fell in between localities where the year of *Mytilus* invasion was known, an estimated year of *Mytilus* invasion was established for a given site by assuming a constant invasion rate between the two nearest localities of known invasion year, and by calculating invasion date as a function of distance from the locality first invaded.

Using these data, the hypothesis that increased food supply is a critical determinant of population increases was tested. There are two key suites of assumptions made in testing this hypothesis: (1) the invasion rate of *Mytilus* is constant between any two given localities of known invasion date, and (2) that time since invasion, *Mytilus* densities and hence food supply for oystercatchers have all been positively correlated since the early 1980s.

The former assumption may not hold in some cases - a study by Branch & Steffani (2004) indicated that localised habitat features do influence the rate at which *Mytilus* spreads. In this study, there was no way to control for such localised habitat effects on *Mytilus* recruitment and this assumption therefore could not be validated. However, there is one line of evidence to suggest that invasion rates are similar over large distances from the points of introduction, Phillips (1994) calculated the invasion rate of *Mytilus* to the west and east of one of its introduction points, at Port Elizabeth. Although the study found a large difference in the rate of spread of *Mytilus* east as opposed to west of Port Elizabeth, and also a large decrease in the rate of spread with the distance from the site of introduction, both these differences were over small scales of approximately 25-30 kilometres from the point of introduction. At larger scales, rates of spread were similar, both east and west of Port Elizabeth, and over stretches of coast further than 25-30 kilometres from the point of introduction. .Given that there are only two points of introduction on the South African coastline from which *Mytilus* has subsequently spread, assuming a constant rate of spread over fairly

large distances (at scales of hundreds of kilometres) for the species may be reasonable for most of the coastal sites where changes in oystercatcher population numbers were calculated.

There is reasonably good evidence to support the second suite of assumptions . A study by Robinson *et al.* (2005) indicates that *Mytilus* biomass is highest in those areas that have been invaded for the longest time. However, this was not statistically tested in the study and may simply reflect higher primary productivity on the west coast, which is also the area first invaded (Bustamante *et al.* 1995). Data linking increased proportions of *Mytilus* in the diet of oystercatchers with improved breeding success and, subsequently with increases in population numbers, are also available from 25 years of monitoring of oystercatcher numbers and dietary changes on west coast islands.

The relative roles of Mytilus *and enhanced protection on oystercatcher populations*

Long-term, breeding-season counts of oystercatchers at eight sites, representing four contrasting scenarios in terms of protection and *Mytilus* status, were used to assess the relative importance of *Mytilus* and protection on changes in adult oystercatcher population numbers. These data series ranged in duration from nine to 28 years, but all spanned virtually the same period between either 1976 and 2004 or between 1979/1980 and 2004. Except for counts during 1979/1980, at all sites, at least two counts were made during each breeding season. In these cases, counts were averaged. Sites included in this analysis were: Jutten and Malgas Islands (both contained within a national park) on the west coast of South Africa, Kommetjie (34°10'S, 18°20'E) and Noordhoek (34°08'S, 18°22'E) on the western seaboard of the Cape Peninsula, and Brandfontein (34°50'S, 19°50'E), De Hoop Nature Reserve (34°29'S, 20°31'E), Gericke's Point (34°02'S, 22°46'E) and Goukamma Nature Reserve (34°02'S, 22°50'E) on the South African south coast (Fig. 1.1).

Due to the small sample size, sites were defined simply as either protected or unprotected and either with or without *Mytilus* at the times of the surveys. A site was defined as protected if it fell within a Marine Protected Area (MPA) as defined by Lombard *et al.* (2004). All sites thus defined have been protected since the early to mid-1980's. Since 2000, there has been a dramatic change in the conservation status of coastal areas outside of MPAs in the form of the nation-wide ORV ban (Department of Environmental Affairs and Tourism 2003, 2004). However, this

change in conservation status has occurred too recently to impact the breeding population (because of delayed maturity), and it is highly unlikely that it has had any significant impact on overall population trends as measured here.

Sites with *Mytilus* present were defined as either areas where *Mytilus* covered >40% of all three mussel zones within the rocky intertidal, as outlined by Robinson (2005) or sites where the proportion of *Mytilus* in the hard-shelled diet of the oytstercatchers formed >40% by number of remains at oystercatcher feeding middens. This distinction had to be made because for two sites – Jutten and Malgas Islands – there were no data on the percentage composition of *Mytilus* in the rocky intertidal, and at the other sites there were very few data on the proportion of *Mytilus* in the birds' diet. It was assumed, however that these two differing criteria were consistent. In one study, the relative abundance of hard-shelled prey items in the feeding middens of African Black Oystercatchers correlated with the relative abundance of the same prey species on the shore (Randall & Randall 1982). Areas lacking *Mytilus* were defined as sites with <5% *Mytilus*. De Hoop and Goukamma Nature Reserves were defined as lacking *Mytilus*, while Kommetjie was defined as having *Mytilus* present (A. Leseberg, D. Loewenthal unpubl. data). There were no site-specific data available for Brandfontein, Gericke's Point and Noordhoek. However, these latter sites lie adjacent to the former three sites, respectively, and were assumed to have similar *Mytilus* status. The latter assumption is validated by an independent study of current *Mytilus* densities around the South African Coast (Robinson *et al.* 2005). In Robinson *et al.*'s (*op. cit.*) study, a total of 27 rocky shore sites sampled randomly on the south coast of South Africa, between Cape Agulhas (34°48'S, 20°02'E) and Tsitsikamma (34°05'S, 23°45'E) (and thus encompassing Brandfontein and Gericke's Point) all had close to zero *Mytilus* biomass, while six of nine randomly sampled sites on the west coast of South Africa, between Elands Bay (32°15'S, 18°20'E) and Cape Point (34°20'S, 18°30'E) (and encompassing Noordhoek) supported mean *Mytilus* biomasses 15 to 20 times higher than at the south coast sites.

Jutten and Malgas Islands were defined as having *Mytilus* present based on the fact that *Mytilus* has formed between *ca* 40% and 80% of the hard-shelled diet of breeding oystercatchers on these islands since the mid 1980s (Hockey & Van Erkom Schurink 1992). Shell middens have been collected at these sites since 1979/80, following the same procedure as described by Hockey & Van Erkom Schurink (1992). The proportion of *Mytilus* in the hard-shelled diet of these populations was

calculated by pooling the data from all middens from both islands and obtaining an overall yearly percentage by number. These data were then added to those from the 1980s already analysed by Hockey and Van Erkom Schurink (1992). In addition to the data on *Mytilus,* data on the ratio of one- to two-chick broods (as a measure of reproductive output) was also analysed for every breeding season since 1992, in the same way as data from the 1980s were analysed by Hockey & Van Erkom Schurink (1992).

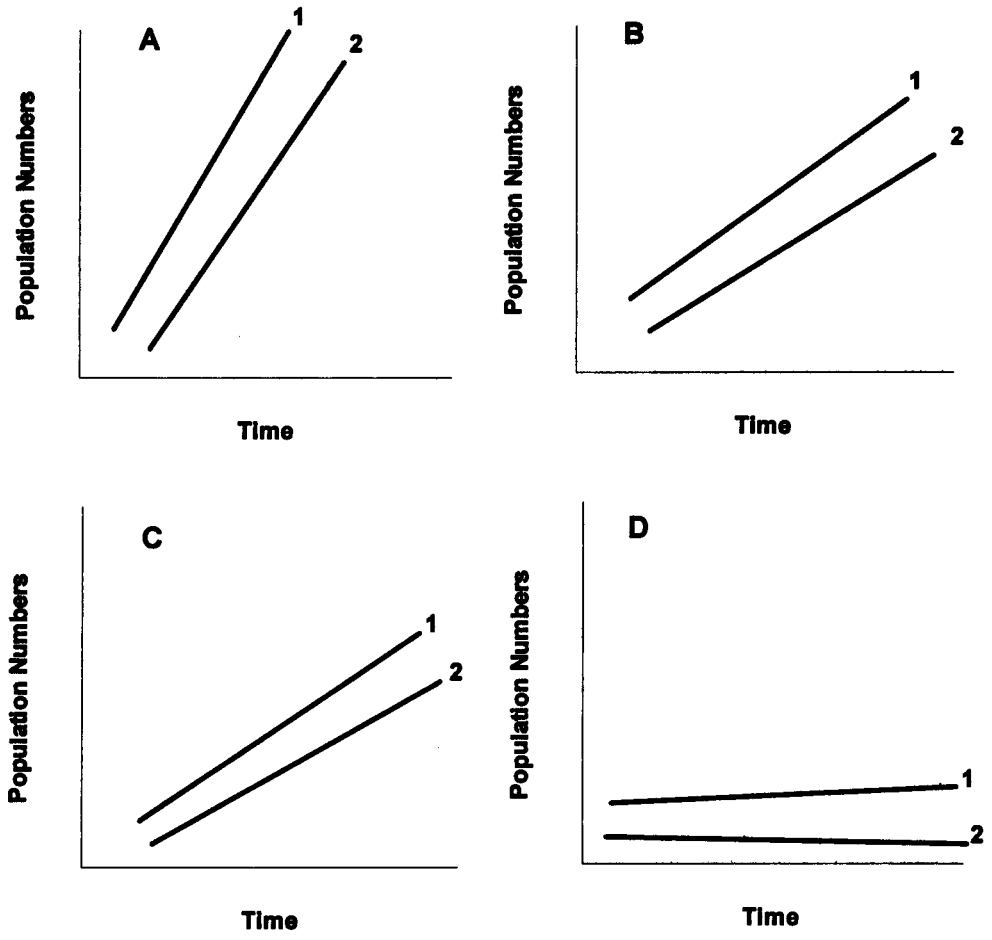

Fig. 2.1: Schematic diagram illustrating the predicted pattern of population changes for oystercatcher populations at sites with A: *Mytilus* and protection (Jutten and Malgas Islands); B: no *Mytilus*, but with protection (De Hoop N.R. and Goukamma N.R.); C: no protection but with *Mytilus* (Noordhoek and Kommetjie); and D: neither protection nor *Mytilus* (Brandfontein and Gericke's Point). 1s and 2s in the diagram refer to populations with the higher and lower rate of increase, respectively.

Based on these data and criteria, treatments were defined as follows: A; protected sites with *Mytilus* present (Jutten and Malgas Islands); B; protected sites lacking *Mytilus* (Goukamma N.R. and De Hoop N.R.); C; unprotected sites with

Mytilus present (Noordhoek and Kommetjie); and D; unprotected sites lacking *Mytilus* (Brandfontein and Gericke's Point) (Fig. 2.1). All sites were chosen based on the fact that they are stretches of coast where oystercatchers feed on rocky shores. Other long-term count data of oystercatcher numbers do exist, but they were not included, because they come from areas where oystercatcher foraging habitat is very different (either sandy shores or lagoonal mudflats). Except for Jutten and Malgas Islands, where oystercatchers typically breed on beds of washed-up shells (Hockey 1992), all sites were characterised by having very similar breeding habitat (namely flat, sandy, kelp-strewn beaches adjacent to, or backing the foraging areas. Thus an effort was made to control for aspects of habitat variability (other than *Mytilus* and protection status). To test the hypothesis that both improved protection status and increased food supply for oystercatchers are the most important factors influencing population changes, the following predictions were made (refer also to Fig. 2.1):

1. Population numbers should have increased at all sites, except in unprotected areas lacking *Mytilus* (treatment D). This assumes that either *Mytilus* in the absence of protection or protection in the absence of *Mytilus* has been sufficient to lead to population increases.

2. For treatment D, populations should either have remained stable or decreased.

3. There should be no significant difference in the rate of population increase between populations with the same *Mytilus* and protection status (e.g. slope A1 = A2, slope B1 = B2, etc).

4. The rate of population increases for treatment A should be greater than that for treatments B or C, because treatment A represents sites that are protected and have *Mytilus* present, whereas treatments B and C are either only protected *or* have *Mytilus* present.

5. The rate of population increases for treatments B and C should both be greater than that for populations represented by treatment D, because treatment D represent sites which are neither protected nor support *Mytilus*, whereas treatment B and C are either protected or have *Mytilus* present.

6. Population changes for treatments B and C should be the same if the potential benefits of *Mytilus* to local oystercatcher populations offset the potential costs of no protection and *vice versa*.

The predictions outlined above assume that *Mytilus* and protection have benefited oystercatcher populations, but do not provide a mechanism for how this benefit might accrue. The evidence from island populations suggests that improved protection and the establishment of *Mytilus* have improved reproductive output (Fig. 2.2) of local populations. However, evidence presented elsewhere (Ch. 5, Ch.7) suggests that local increases may largely be due to increased settlement of previously excluded sexually mature birds. Nevertheless, both reproductive output (Fig. 2.2) and settlement rates (Ch. 7) may be influenced by both *Mytilus* and protection. In this study the mechanism by which local population increases may have occurred is not explicitly addressed. It is assumed that the same predictions hold, regardless of the mechanism(s) involved. For populations lacking both protection and *Mytilus*, numbers are predicted to have either decreased *or* remained stable. The reason for this prediction is that if lack of *Mytilus* and protection resulted in unsustainably low reproductive rates, these may not be reflected in a population decrease because low reproductive rates may be masked by high adult longevity, given the time period over which population trends were assessed (Ch. 5, Ch. 6).

To test predictions 1 and 2 above, linear regressions were fitted to all count data. To test prediction 3 above, the slopes of the regressions (i.e. rate of population increases) were compared statistically between the two populations within each treatment (i.e. between A1 and A2, B1 and B2, etc.). To test prediction 4 above, in the first instance A2 was compared with each of B1 and C1. This was based on the logic that if the population with the lower rate of increase for treatment A (A2) had a significantly higher rate of increase than did the populations with the higher rates of increase for treatments B (B2) and C (C2), then all other sets of comparisons between population increases for treatments A, and for treatments B or C could be assumed to yield a similar result and need not be tested statistically. These initial comparisons yielded a significant result in each case and thus no further combinations for treatments A, B and C were compared.

Similarly, to test prediction 5, in the first instance B2 and C2 were each compared with D1. These comparisons yielded significant difference for B2 compared with D1, but not with C2 and D1. Consequently C1 was compared with D1, but there was no difference here either and statistical comparison between treatments B, C and D were stopped at this point. (Because there was found to be no statistically significant increase for population D2, while there were significant increases for all the other sites, D2 was not compared statistically with population trends from any of the other sites).

To test prediction 6, population changes for treatments B and C were also statistically compared to assess whether the potential benefits of *Mytilus* offset the potentially negative impacts of a lack of protection. Because there was no *a priori* reason to assume that one site should have experienced more rapid increases in bird numbers than the other, all population increases (i.e. slopes of the regressions) from sites B and C were compared using an F-test for regression coefficients and followed up by Tukey's post-hoc tests on individual pairs of sites to assess where significant differences existed.

RESULTS

Population trends

Trends on the mainland within Sub-regions

Namibia: Numbers of oystercatchers on the Namibian coast apparently decreased from 506 to 379 between the early 1980s and the present (Table 2.1). However, historically, 300 birds were estimated (rather than counted) along the stretch of coast between Grossebucht, Lüderitz and the Orange River (236 km) (Hockey 1983a), whereas only 103 were counted on this stretch of coast during the recent aerial survey.

Whilst decreases have been demonstrated for one small area within this stretch at Elizabeth Bay (26°54'S, 15°12'E), almost certainly due to mining activities, all other areas surveyed in the same study showed stable or increasing numbers (Simmons 2005). It is therefore likely that the historical figure of 300 (Hockey 1983a) was an overestimate.

Northern Cape: Recent surveys recorded 79 birds for this stretch of coast, compared with 86 birds estimated from historical surveys (Table 2.1). Values are very close and given that historical data were based on estimates rather than absolute counts, this difference is unlikely to be significant.

Table 2.1. Trends in numbers of African Black Oystercatchers on the mainland. Relevant sample sizes (N) are given in parentheses next to each *Sub-region.* Significant p-values are highlighted. KR = Kunene River; ORR = Orange River; OLR = Olifants River; CP = Cape Point; MB = Mossel Bay; PE = Port Elizabeth; KR = Kei River; RA=Ramsgate. [Note: only single counts were made in each time period on the coastline between the Kunene River and the Olifants River, and between the Kei River and Ramsgate: differences between these counts could therefore not be tested statistically.]

	Shore length	1978 - 1980		1997 - 2002		Trends	
Sub-region	(km)	Count	Birds.km^{-1}	Count	Birds.km^{-1}	$t_{a(1)}$	p-value
KR – OR	1520	506	0.33	379	0.25	-	-
OR – OLR	175	86	0.49	79	0.45	-	-
OLR. – CP (57)	387	949	2.45	1264	3.26	583.5	>0.05
CP – MB (44)	284	394	1.38	677	2.38	183.5	**<0.01**
MB – PE (35)	241	315	1.31	726	3.01	57.5	**<0.001**
PE – KR (19)	271	315	1.16	637	2.35	11	**<0.001**
KR - RA	192	25	0.13	43	0.22	-	-
Totals	**3071**	**2590**	**1.04**	**3805**	**1.70**	-	-

Olifants River to the Kei River, South Africa: The mainland oystercatcher population for this entire stretch of coast has increased significantly ($t_{(1),155}$ = 2 157, p<0.001) by >1300 birds since the 1980s. Oystercatcher densities remain highest along the west coast of South Africa, with the *Sub-region* between the Olifants River and Cape Point supporting the highest average density (3.26 birds.km^{-1}, Table 2.1). Interestingly, this *Sub-region* also had the lowest (and a statistically insignificant) proportional increase compared to all other *Sub-regions* (Table 2.1). The largest increases have occurred between Mossel Bay and Port Elizabeth, where populations have more than doubled in 25 years (Table 2.1).

Former Transkei: Numbers have increased from 23 to 43 birds between the Kei River and Ramsgate. During historical surveys, no birds were recorded east of the Dwesa-Cwebe Reserve (32°18'S, 28°50'E), while during the recent survey birds were observed as far as 3 km west of Ramsgate, *ca* 220 km further east.

If minimum counts based on recent surveys are considered, then changes in numbers of oystercatchers over all these regions indicate an increase of at least 1 215 birds for oystercatchers on the mainland coast of Southern Africa.

Islands

Namibia: Numbers of oystercatchers on Namibian islands have increased by 181 birds over the past 20 years, primarily due to a large increase on Possession Island, where the population has increased by more than 100 birds (Table 2.2). All other Namibian island populations appear to have remained fairly stable, except those on Flamingo Island. However, the Flamingo Island count, especially in the light of low counts from nearby Seal and Penguin Islands, probably represents a high-tide roost. Flamingo Island is very small, is connected to the mainland at low tide and could not possibly support a resident oystercatcher population of >140 birds. Oystercatchers do move regularly between Flamingo, Seal, Penguin and Shark Islands (P.A.R. Hockey pers. comm.). Treated as a unit, these four islands have shown a population increase of only 12 birds, which is unlikely to be significant.

Western Cape: Virtually all island populations in this region have undergone marked increases. The exceptions are Meeuw Island (a decrease of two birds), and Marcus Island, where there was a steady decrease in numbers from the early 1980s until the mid 1990s. This decrease and lack of recovery is due to the impacts of terrestrial predators, a result of the island being connected to the mainland by a causeway (Cooper *et al.* 1983, Hockey 1983a).

Eastern Cape: In comparison to populations on the islands in the Western Cape, numbers on islands in this region have remained virtually unchanged over the past 20 years (Table 2.2).

Population changes in relation to habitat

Mixed shores: On the mainland coast between the Olifants the Kei Rivers, mixed shores currently support the greatest number of oystercatchers (1678±44), representing an increase of 815±44 birds. [Note: S.D. values are the same for recent counts and for changes in numbers, because only one historical count was available

Table 2.2. Counts of African Black Oystercatchers and population changes on the offshore islands of southern Africa

Region	Island	Historical Count	Recent Count	Difference
Namibia	Mercury	2	6	4
	Ichaboe	3	23	20
	Marshall Rocks	0	0	0
	Staple Rocks	0	0	0
	Dumfudgeon Rocks	2	0	-2
	Flamingo	10	142	132
	Seal	97	6	-91
	Penguin	55	34	-21
	Shark	8	10	2
	Halifax	71	77	6
	North Long	2	1	-1
	Lady's Rocks	0	0	0
	North Isle	5	-	-5
	Possession	281	386	105
	Albatross Rocks	3	2	-1
	Pomona	24	60	36
	Plumpudding	8	7	0
	Sinclair	5	1	-3
Total		**574**	**755**	**181**
South Africa	(Unamed Islands)	14	-	-14
Western Cape Province	Bird (Lambert's Bay)	1	3	2
	Malgas	66	129	63
	Marcus	123	65	-58
	Jutten	175	234	59
	Schaapen	23	25	2
	Meeuw	10	8	-2
	Vondeling	78	117	39
	Dassen	221	339	118
	Robben	40	166	126
	Seal (False Bay)	1	-	-1
	Geyser	1	-	-1
	Dyer			
Total		**788**	**1143**	**355**
Eastern Cape Province	Seal (Mossel Bay)	0	9	9
	St. Croix	16	20	4
	Bird Island Group	14	14	0
Total		**30**	**43**	**13**
Island Total		**1406**	**1941**	**535**

for comparisons]. All mixed-shore *Sections* have experienced increases in Oystercatcher numbers (Table 2.3). Mixed shores on the west coast of South Africa (between Slipper Bay and Cape Point) support the greatest number of birds, but the

Table 2.3. Counts of African Black Oystercatchers on mixed shores on *Sections* between the Olifants River and the Kei River. (Shore length to the nearest km).OLR = Olifants River; SB = Slipper Bay; CP = Cape Point; CA = Cape Agulhas; MB = Mossel Bay; TR = Tsitsikamma River; PE = Port Elizabeth; CPA = Cape Padrone, KR = Kei River. % Shore ext. = percentage of the shore extrapolated. Ext. factor = extrapolation factor.

	Real counts			Extrapolated counts (1997 – 2002)				
	Shore length (km)	1979/1980 count	1997-2002 mean count	-2 S.D.	Mean	+2 S.D.	% Shore ext.	Ext. factor
OLR – SB	35	35	91	-	91	-	0	-
SB – CP	93	428	591	-	591	-	0	-
CP – CA	48	61	81	-	81	-	0	-
CA – MB	70	68	75	264	289	315	67	4.47
MB – TR	34	56	114	-	114	-	0	-
TR-PE	39	25	90	-	90	-	0	-
PE – CPA	9	18	40	-	40	-	0	-
CPA – KR	178	172	350	364	382	400	7	4.04
Total	**506**	**863**	**1432**	**1635**	**1678**	**1722**	-	-

largest increases have been between Cape Agulhas and Mossel Bay. The population at the eastern extremity of the breeding range, between Cape Padrone and the Kei River, has also increased substantially (Table 2.3). On average, the proportion of shoreline where counts on mixed shores had to be extrapolated within *Sections* was less than 10%.

Rocky shores: Increases in oystercatcher numbers on rocky shores were less than on other shore types: this habitat also supported the lowest overall densities of oystercatchers. Rocky shores do, however, appear to support far more (355±65) oystercatchers now then they did historically, but there may be a substantial error in

the estimate, because on average, numbers on 39% of the shoreline had to be extrapolated to arrive at the overall population size (Table 2.4). Most of the shoreline where counts were made was gently sloping: such shores are likely to support much

Table 2.4. Counts of African Black Oystercatchers on rocky shores within *Sections* of the coast between the Olifants River and the Kei River. (Shore length to the nearest km.). OLR = Olifants River; SB = Slipper Bay; CP = Cape Point; CA = Cape Agulhas; MB = Mossel Bay; TR = Tsitsikamma River; PE = Port Elizabeth; CPA = Cape Padrone, KR = Kei River. % Shore ext. = percentage of the shore extrapolated. Ext. factor = extrapolation factor.

	Real Counts			Extrapolated Counts (1997 – 2002)				
	Shore Length (km)	1979/1980 count	1997/2002 mean count	-2 S.D.	Mean	+2 S.D.	% Shore ext.	Ext. factor
OLR – SB	45	12	26	25	26	27	45	0.91
SB– CP	122	216	313	304	336	368	41	2.60
CP – CA	134	153	196	291	303	314	56	1.63
CA – MB	103	150	154	193	204	216	51	1.31
MB – TR	41	45	56	56	60	64	38	1.06
TR – PE	16	19	11	13	13	13	19	0.71
PE – CPA	14	12	4	9	9	9	7	0.72
CPA – KR	29	22	27	28	33	37	55	2.75
Total	**504**	**629**	**787**	**919**	**984**	**1048**	-	-

higher densities of birds than, for example, coastal cliffs or areas where rocks plunge steeply into the sea (Hockey 1983a). Thus, apparent increases are likely to be overestimates for this shore type. Increases in numbers along the west coast were due largely to increases on the Vredenburg Peninsula, north of Saldanha Bay. The increases here are also likely to be inflated, because adjacent islands (particularly Malgas and Jutten Islands), support very high breeding densities and sub-adult birds reared on islands and queuing for breeding opportunities use adjacent mainland coasts (Hockey 1983a) but do not breed there (this study).

Sandy shores: The average proportion of sandy shoreline for which counts had to be extrapolated was 31%. Based on this, numbers on sandy shores have increased by 480±138 birds (Table 2.5). Numbers on the west coast of South Africa, between the Olifants River and Cape Point, have remained fairly stable (counts indicate decreases, but these are small in relation to the total population size and are unlikely to be significant), while on the south and east coasts of South Africa, numbers on rocky shores have increased dramatically, with the stretch of coast between the Tsitsikamma River and Port Elizabeth supporting 226±5 more oystercatchers than previously.

Table 2.5. Counts of African Black Oystercatchers on sandy shores within *Sections* of the coast between the Olifants River and the Kei River. (Shore length to the nearest km). OLR = Olifants River; SB = Slipper Bay; CP = Cape Point; CA = Cape Agulhas; MB = Mossel Bay; TR = Tsitsikamma River; PE = Port Elizabeth; CPA = Cape Padrone, KR = Kei River. % Shore ext. = percentage of the shore extrapolated. Ext. factor = extrapolation factor.

	Real counts			Extrapolated counts (1997 – 2002)				
	Shore length (km)	1979/1980 count	1997/2002 mean count	-2 S.D.	Mean	+2 S.D.	% Shore Ext.	Ext. factor
OLR – SB	125	91	63	-	63	-	0	-
SB – CP	107	231	180	183	209	236	18	1.34
CP – CA	92	46	51	40	73	107	55	2.28
CA – MB	81	83	116	129	137	146	33	1.54
MB – TR	80	41	94	74	112	150	23	4.47
TR– PE	52	109	335	330	335	340	15	3.29
PE – CPA	77	111	207	200	207	214	7	4.96
CPA – KR	17	14	-	49	69	90	1	4.96
Total	**630**	**726**	**1046**	**1068**	**1205**	**1346**	-	-

Together, all three habitat types on the mainland between the Olifants River and the Kei River are estimated to support 3 867±248 oystercatchers, more than double the population size in the early 1980s (*ca* 1650 birds). Currently, within these geographical limits, mixed, sandy and rocky shores respectively support 42%, 31% and 24% of the total oystercatcher population. All extrapolated values were

considered reasonable to conservative, except for the high extrapolation factor (4.47) applied to mixed shores in the *Section* between Cape Agulhas and Mossel Bay which may have resulted in a considerable overestimate of the population size for the mixed shore south of Waenhuiskrans, near Arniston (20°15'S, 34°39'E). However this overestimate is negligible in terms of its impact on the total population estimate for this shore type (90 oystercatchers were predicted to be present in an area that previously supported only 26).

The majority of birds still occur on the mainland (although islands remain, relative to their size, disproportionately important breeding refuges). The ratio of island population size to mainland population size remains very similar to what it was in the early 1980s. Historically, 69% of the population (3185 birds) occurred on the mainland: this has increased slightly to 71% (4729 birds). The Western Cape remains the most important region as far as representation of the global population is concerned (unchanged from 37% of the total), while the greatest absolute and proportional increases have occurred in the Eastern Cape (Table 2.6).

Table 2.6. Regional summary of oystercatcher numbers based on historical and recent surveys. N = Namibia; NCP = Northern Cape Province; WCP = Western Cape Province; ECP = Eastern Cape Province; FT = Former Transkei.

Locality	Mainland coast		Islands		Coastal wetlands		Total	
	1979/ 1980	1997/ 2002	1979/ 1980	1997/ 2002	1979/ 1980	1997/ 2003	1979/ 1980	1997/ 2003
N	506	379	574	755	89	163	1169	1297
NCP	86	79	14	-	26	0	126	79
WCP	1574	2403	788	1143	133	98	2495	3644
ECP	644	1464	30	43	104	100	778	1607
FT	23	43	0	0	0	0	23	43
Total	**2833**	**4368**	**1406**	**1941**	**352**	**361**	**4591**	**6670**
	56%	55%	56	58	37	27		54%

The global population size

The current global population size of African Black Oystercatchers is estimated at *ca* 6670 birds. This represents an increase of 46% (>2000 birds) over the past 20 years (Table 2.6).

The influence of *Mytilus* and protection on oystercatcher numbers

Ongoing monitoring of oystercatcher diet, chick broods and population numbers on Malgas and Jutten Islands since 1992 have indicated that subsequent to the increase in oystercatcher productivity, there has been a large increase in population numbers. However, the increase in population numbers appears to have started approximately six years after productivity peaked in the late 1980s/early1990s. During the period when oystercatcher numbers were increasing, the productivity of these populations appears to have decreased and stabilised at a level similar to that at the time at which *Mytilus* first established itself in the late 1970s/early 1980s (Fig. 2.2). Population numbers on these islands have been fairly stable since the late 1990s. The proportion of *Mytilus* in the diet of oystercatchers has stabilised since the mid-1990s, as has the ratio of one- to two-chick broods (Fig. 2.2).

Year of Mytilus *invasion and population-wide trends*

Despite the fact that data from the Saldanha Bay islands strongly support a link between *Mytilus* and an increase in oystercatcher population numbers, population-wide assessment of the influence of *Mytilus* on oystercatcher populations on rocky and mixed shores revealed no significant relationship between increases in oystercatcher population size (measured either as a total, density or proportional increase) and estimated year of *Mytilus* invasion (Table 2.7).

Table 2.7. Regression coefficients (r-values) for the change in oystercatcher numbers with years since the *Mytilus* invasion.

Trend	Mixed Shores	Rocky Shores	Mixed & Rocky Shores
Total Numbers	0.02	0.12	0.06
Density	0.07	0.09	0.05
Proportion	0.15	0.32	0.06

The relative influence of Mytilus *and protection on oystercatcher populations*

Comparisons of population trends from long-term data sets strongly support the contentions that a) *Mytilus* has benefited oystercatchers by increasing food availability, and b) increased protection since the early to mid-1980s has also been reflected in population increases.

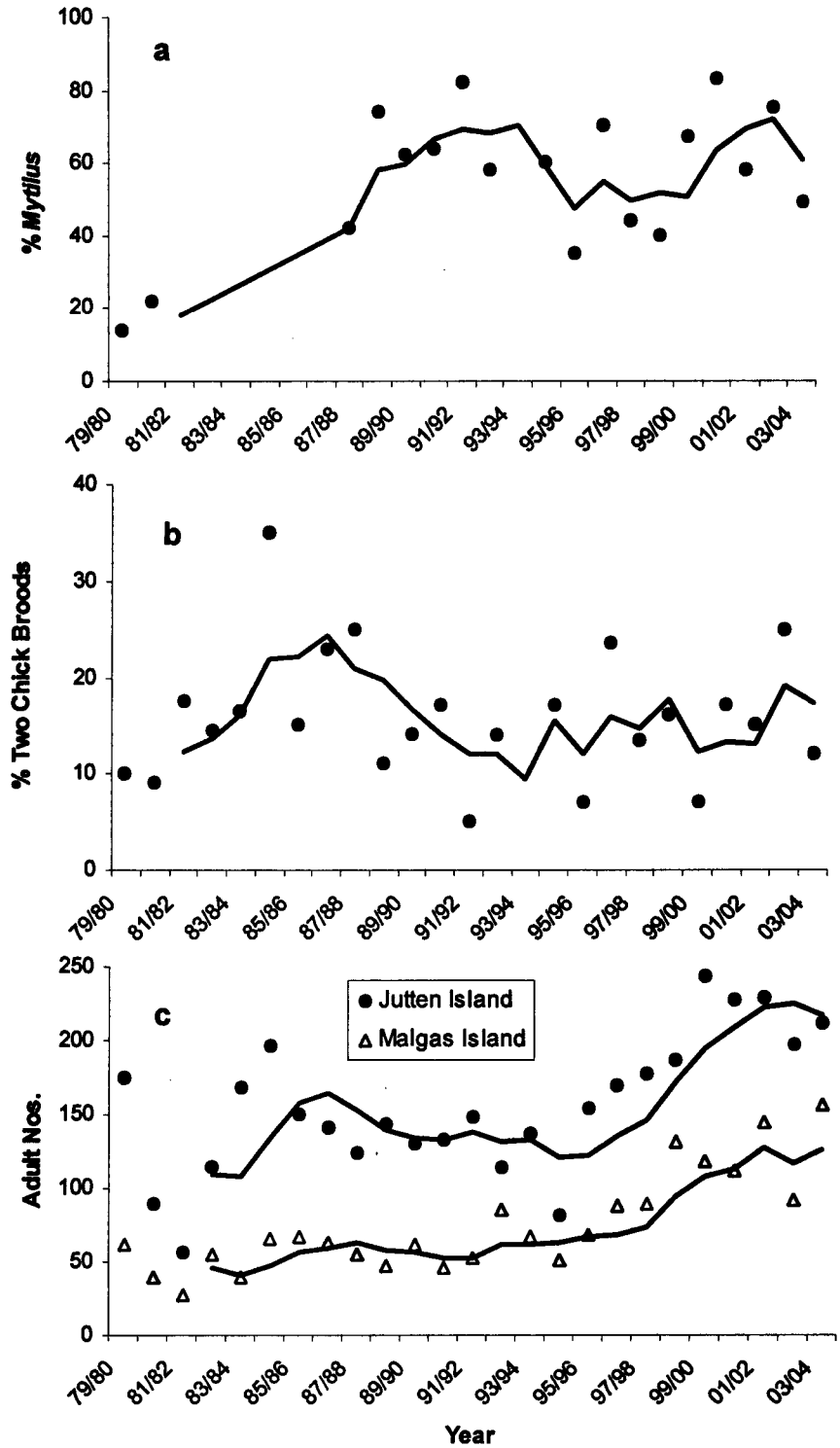

Fig 2.2. a) Changes in the proportion of *Mytilus* in the hard shelled diet of oystercatchers: b) concomitant changes in the proportion of two-chick broods and c) population numbers of oystercatchers on Jutten and Malgas Islands (data on % 2-chick broods and % *Mytilus* are pooled for the two islands and trend lines reflect 3-year moving averages).

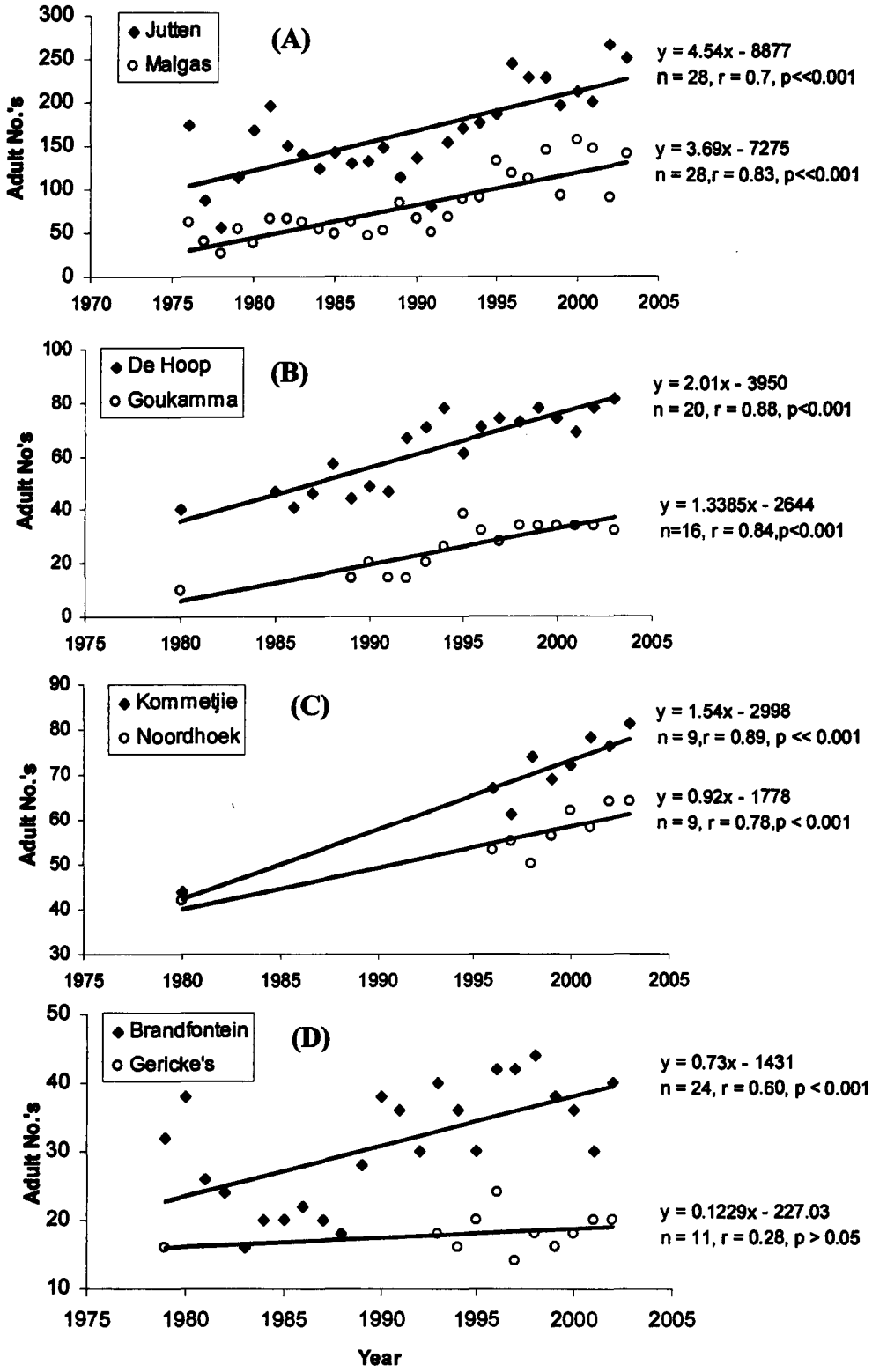

Fig 2.3. Trends in adult oystercatcher numbers for the treatments defined as: (A) Protected, with *Mytilus* present, (B) Protected, lacking *Mytilus*, (C) Unprotected, with *Mytilus* present, and (D) Unprotected, lacking *Mytilus*.

At all sites, except for Gericke's Point (which is unprotected and lacks *Mytilus*), there have been significant increases in oystercatcher numbers. However, the rate at which populations have increased have differed between protected and unprotected sites, and between areas with and without *Mytilus* (Fig. 2.3).

As predicted, there were no differences in population growth rates for most within-treatment comparisons, except in the case of Noordhoek and Kommetjie (Table 2.8). Populations at Malgas (protected, with *Mytilus*) have increased more rapidly than populations at either De Hoop (protected, lacking *Mytilus*) or Kommetjie (unprotected, with *Mytilus*), suggesting that, in concert, both *Mytilus* and protection significantly benefit oystercatchers (Table 2.8). The benefit of protection, even in the absence of *Mytilus*, is born out by the fact that populations at Goukamma Nature Reserve (protected, lacking *Mytilus*) have increased more rapidly than at Brandfontein (unprotected, lacking *Mytilus*). However, it was not possible to demonstrate the reverse situation: populations at Noordhoek (unprotected, with *Mytilus*) have not increased more rapidly than at Brandfontein (Table 2.8).

There were significant differences in oystercatcher population trends between unprotected sites with *Mytilus* and protected sites lacking *Mytilus* ($F_{3,46} = 3.28$, $p < 0.05$). Post-hoc tests revealed that these were due to differences in trends between only two of these sites, namely Noordhoek (unprotected, with *Mytilus*) and De Hoop

Table 2.8. Comparisons of population trends in adult oystercatcher numbers between sites with similar protection and *Mytilus* status and between sites with differing protection and *Mytilus* status. UP=Unprotected, P = Protected, PM=Protected with *Mytilus* present, UPM = Unprotected with *Mytilus* present.

Sites (Within "Treatment" Comparisons)	d.f.	$t_{\alpha(2)}$	p
Brandfontein(UP) & Gericke's(UP)	31	1.57	>0.05
De Hoop(P) & Goukamma(P)	32	1.91	>0.05
Noordhoek(UPM) & Kommetjie(UPM)	14	2.33	<0.05
Malgas(PM) & Jutten(PM)	52	0.84	>0.05
Sites (Between "Treatment" Comparisons)	**d.f**	$t_{\alpha(1)}$	**p**
Goukamma(P) & Brandfontein(UP)	36	1.79	<0.05
Noordhoek (UPM) & Brandfontein (UP)	29	0.59	>0.05
Malgas(PM) & De Hoop(P)	44	2.31	<0.025
Malgas(PM) & Kommetjie(UPM)	33	1.88	<0.05

(protected, lacking *Mytilus*) ($q_{3,25} = 3.71$, $p < 0.025$), further suggesting that protection status and *Mytilus* status as defined here are likely to explain most of the

variation in population trends. Long-term trends thus generally support the contention (originally supported by data from the Saldanha Bay Islands - Fig. 2.2) that both *Mytilus* and protection have benefited oystercatcher populations.

Easterly range extension

In addition to the increases in oystercatcher numbers within their historical breeding range, it appears that the birds are undergoing an eastward range expansion: whether this represents a genuine range expansion or recolonisation of areas previously occupied is unclear. The reason for this uncertainty is that historical data are sketchy in the extreme. Accounts of oystercatchers in the Eastern Cape and KwaZulu-Natal region first appeared in the literature about 130 years ago, but these were purely anecdotal. Layard (1867) mentioned oystercatchers being present at Port Elizabeth and East London, but not plentiful at either place, and very scarce in Natal, while Clancey (1964) mentions an oystercatcher sighted near Durban in 1953. However, given both current data from the Eastern Cape and observations of breeding and non-breeding birds in KwaZulu-Natal, there is now convincing evidence for a recent range expansion (Brown & Hockey 2007). Prior to 1983, there were only four records of oystercatchers east of the former Transkei, with the most northerly being from Mtunzini, Kwazulu-Natal (Hockey 1983a). No breeding birds had been recorded in KwaZulu-Natal, and the most easterly breeding record was from Mazeppa Bay, Eastern Cape (32°28'S, 28°39'E) (Hockey 1983a). However, since then there has been a substantial increase in numbers in the Eastern Cape (Vernon 2004, N. Smith unpubl. data) and pairs have bred at two localities in southern KwaZulu-Natal since the late 1990s (Nevill 1999, M., K. & B. Nicholson *in litt.*, Brown & Hockey 2007). The eastern limit of vagrancy has also been extended. The most easterly record of vagrancy prior to 1996 was from Dawson's Rock (28°38′S, 32°18′E) (Hockey & Douie 1995), but there has subsequently been a record from Inhaca Island, Mozambique (Parker 1999). In total there are 31 localities in KwaZulu-Natal where oystercatchers were sited between 1998 and 2006. Most sitings consisted of between one and three birds (including the two breeding pairs), but roosts of up to 10 birds have been observed at Umkomaas Beach (30°12′S, 30°48′E) (Brown & Hockey 2007). Data from KwaZulu-Natal were not included in the current reassessment of the global population. However, based on minimum and maximum numbers over the

period 1998-2006 at the 31 localities are taken into account, this represents between 71 and 148 birds in KwaZulu-Natal.

DISCUSSION

The global African Black Oystercatcher population has increased by more than 2000 birds over the last 20-25 years. Analyses of population trends and current oystercatcher densities, by shore type, as well as comparisons of long-term trends in areas with and without *Mytilus* and with and without protection, suggest that both the *Mytilus* invasion and enhanced protection have benefited oystercatcher populations. Unexpectedly, when spatially extensive data were analysed, the regional timing of *Mytilus* invasion was a poor predictor of population changes. However, detailed long-term monitoring data from localities with or without *Mytilus*, and with or without protection, strongly support the conclusion that *Mytilus* has had a positive influence on oystercatcher populations around the coast (Fig. 2.3), as do the dietary and productivity data from the Saldanha Bay Islands (Fig. 2.2). It is possible that time since invasion does not necessarily translate into uniformly increasing mussel density, which may be inferred from the unequal rates of spread between known points of establishment (Branch & Steffani 2004). Another possibility is that the predicted pattern is obscured by source-sink dynamics, with saturated areas that have an over-production of young exporting birds to suboptimal habitats. Although the latter scenario is possible, it appears to be unlikely given the extremely high levels of natal philopatry (Ch. 5).

Although the analysis of long-term population trends mostly confirmed predictions with regard to the effects of *Mytilus* and protection, there was one notable exception. The increase in numbers at the unprotected Noordhoek site, where *Mytilus* is present, was no greater than at the unprotected Brandfontein site, which lacks *Mytilus*. The Noordhoek site is heavily disturbed (see below), and the negative effects of human disturbance may have negated potential benefits to be gained from the presence of *Mytilus*. This conclusion is strengthened by the fact that the 'within treatment' comparison of population trends at Noordhoek and nearby Kommetjie indicated significant differences between these two sites (where it was predicted that there should be none if *Mytilus* and protection status are the main agents driving population changes). Furthermore, the comparison of the two groups of treatments

which represented either areas with *Mytilus* and without protection or *vice versa*, were significantly different. This was due to a significant difference in population trends between Noordhoek and De Hoop N.R..

Differences between trends at Noordhoek and De Hoop N.R. are likely to be a consequence of localised habitat effects. Noordhoek is in a more productive region of the coast (Bustamante *et al.* 1995) and in an area with much higher *Mytilus* densities (Robinson *et al.* 2005). However, the rocky shore is less suited to oystercatchers, comprising mostly boulder fields, rather than the favoured wave-cut rocky platforms that predominate at De Hoop N.R. (Hockey 1983a). The area backing the rocky intertidal at Noordhoek is ideal breeding habitat for oystercatchers, yet oystercatchers are forced (by virtue of disturbance) to breed on a nearby sandy beach, adjacent to the rocky shore. Historically, they probably did breed adjacent to the foraging area (and one pair has been observed attempting to do so (pers. obs.), although invariably unsuccessfully), but the level of human disturbance is very high, with a housing development directly behind the beach. Because pairs are distributed linearly along the adjacent sandy shore, when feeding chicks, adults have to fly large distances back and forth to deliver food (pers. obs.). For a bird that's life-history makes chick rearing a relatively expensive process in energetic terms (Leseberg *et al.* 2000), this probably impacts on fledgling production and, ultimately, on population growth rate.

While a combination of *Mytilus* and protection appear to be largely responsible for the very rapid increases in population numbers at Jutten and Malgas Islands, the potential benefits of relatively low levels of predation also need to be considered. Jutten and Malgas Islands are free of terrestrial predators and have been for at least the last 30 years. Historically, introduced mammals on islands have had severe impacts on oystercatchers (Cooper *et al.* 1983, Hockey 1983a). On the mainland, predation in both protected and unprotected areas probably accounts for more than 50% of all chick mortality in the first week after hatching (Ch. 3). In protected mainland areas, Small Grey Mongooses *Galerella pulverulenta*, Small-spotted Genets *Genetta genetta* and Large-spotted Genets *G. tigrina* appear to be the most important predators (Cape Nature Conservation 2004, Oystercatcher Conservation Programme unpubl. data), whereas at disturbed sites, domestic dogs *Canis familiaris* appear to be the most important predators of young chicks (Hockey & Loewenthal 2002). Oystercatcher populations on islands do experience predation of eggs and chicks by Kelp Gulls *Larus dominicanus* (pers. obs.). Although the impacts

of gull predation on island-breeding African Black Oystercatchers has not been quantified, at least one study has demonstrated that gulls have a significant predation-related impact on island-breeding populations of Eurasian Oystercatchers and that removal of gulls resulted in a large increase in the breeding population (Harris & Wanless 1997). However, at Jutten Island, despite a substantial increase in the size of a breeding colony of Kelp Gulls over the past *ca* 25 years (Crawford *et al.* in press) the rate of the oystercatcher population increase was the same as that on Malgas Island, which has a far lower density of resident, breeding Kelp Gulls (Crawford *et al.* in press). Population trends from two other islands - Robben Island and Dassen Island - also suggest that the effect of predation has not compromised the beneficial effects of *Mytilus* and protection. On Dassen Island, terrestrial predators, mainly domestic cats *Felis catus* have been and are still present (J. Visagie pers. comm.), while on Robben Island cats, dogs and House Rats *Rattus rattus* are all present (Calf & Underhill 2002) and likely to impact the most important breeding sites on the island. Both of these islands lie within a few kilometres of the west coast mainland of South Africa where *Mytilus* invaded between 1979 and 1981 (Robinson 2005). At Dassen Island there has been a 65% increase in oystercatcher numbers (from 221 in 1979/1980 to 339 in 2003/2004), while at Robben Island there has been nearly a four-fold increase (from 40 in 1977 to *ca* 175 in 2001/2002 - Calf & Underhill 2002). Extensive beds of *Mytilus* occur on rocky shores at Dassen Island (D. Loewenthal pers. obs., A. Wolfaardt., J. Visagie pers. comms.), while on Robben Island *Mytilus* covers approximately 40% of the low shore (Tjørve & Underhill 2006). Both islands are protected, although Robben Island much less so. Dassen Island is not accessible to the public, while Robben Island is a World Heritage Site (UNESCO 1999) and significant tourist attraction. The island qualifies as a RAMSAR site and several recommendations have been made to protect breeding oystercatchers from the potentially negative effects of human disturbance as a result of increased tourism (Calf & Underhill 2002).

Although *Mytilus* is known to have invaded (at least temporarily) one soft-sediment site, on sand banks within Langebaan Lagoon (33°09'S, 18°03'E) (Robinson & Griffiths 2002), it has always been and continues to be primarily a rocky shore invasive (Hockey & Van Erkom Schurink 1992, Robinson *et al.* 2005). Given that it has been established for much longer on the west coast than on the south coast and occurs in much higher densities in the former area (Robinson *et al.* 2005), it was

predicted that any upward trend in oystercatcher numbers would be most pronounced on the west coast, as opposed to the south coast. Although local trends in oystercatcher numbers do suggest a strong link between *Mytilus* biomass and increases in numbers, this prediction was not validated at larger spatial scales. For example, the *Sub-region* between the Olifants River and Cape Point supported the highest number (1264) and density (3.26 birds.km^{-1}) of oystercatchers, but the proportional increase was not as great as on the south coast, where numbers between Cape Point and the Kei River have nearly doubled. It is possible that oystercatcher numbers along the west coast mainland of South Africa were already approaching saturation levels by the early 1980s, although this seems unlikely when compared with population trajectories at west coast islands (Fig. 2.2). Perhaps a more plausible explanation is that there has been an unequal trade-off between the two putative agents of increases in oystercatcher populations (protection and increased food supply). A far greater proportion of the south and east coasts (relative to the west coast) falls within Marine Protected Areas (MPAs) (Lombard *et al.* 2004) and the proportion of the oystercatcher population within MPAs is concomitantly smaller on the west coast (Hockey *et al.* 2000). Outside of these MPAs there have been numerous coastal developments on the west coast, many of which, even recently, have been approved without Environmental Impact Assessments (Rao 2005). In many of these cases, developments physically alter the shoreline – even below the high-water mark (pers. obs.). A case in point is the construction of informal settlements on a 12.6 km stretch of shore on the west coast of South Africa near the town of Vredenburg (32°54'S 17°59'E). Despite the fact that this stretch of shore provides ideal breeding and feeding habitat for oystercatchers, there has been a 63% decrease in numbers over the past 25 years, while regionally, numbers on the mainland have increased by 24% over the same period (P.A.R. Hockey unpubl. data). It may be that disturbance-related phenomena have prevented oystercatchers from reaching a new (food-linked) saturation density.

On the other hand, the south and east coasts between Cape Point and the Kei River have much lower densities of *Mytilus* (Robinson *et al.* 2005), although *Mytilus* has been recorded in significant densities on rocky shores as far east as Kidd's Beach (33°08'S, 27°41'E). It could be argued that even at these low levels, *Mytilus* has had significant benefits for foraging oystercatchers and that this, together with improved protection, has resulted in the larger proportional increases along this section of coast,

compared with the west coast. However, analyses by shore type indicate that on sandy shores (which lack *Mytilus*) on the south coast and even more so on the east coast, oystercatcher numbers have increased dramatically over the past 25 years (Table 2.5). For example, between the Tsitsikamma River and Port Elizabeth numbers on sandy shores have nearly doubled over this period. While it is likely that there has been some shift of the population onto sandy shores (particularly from some mixed shores where there has been an even more dramatic increase in numbers, e.g. nearly a four-fold increase between the Tsitsikamma River and Port Elizabeth (Table 2.3)), there is another important aspect to consider with regard to food availability. On sandy shores oystercatchers prey largely on white mussels (*Donax* spp.), especially *Donax serra* (Hockey 1981). Although white mussels are common on both the west and the south and east coasts, their littoral distribution is very different. On the west coast they occur predominantly subtidally, while on the south and east coasts they are concentrated around the mid-tide mark (Branch *et al.* 1994). This higher prey availability on sandy shores on the south and east coasts, as opposed to the west coast, is reflected in much higher oystercatcher densities. Based on real counts (rather than extrapolated values), oystercatcher densities on sandy shores in 1979/1980 averaged 0.49 birds.km^{-1} between the Olifants River and Cape Point, whereas from Cape Point east to the Kei River, the density was 0.91 birds.km^{-1}. Due to a differential increase in population numbers on sandy shores in the latter two regions over the past 25 years, the difference is now even more pronounced. For the same areas, the densities are calculated to be 0.31 birds.km^{-1} and 1.89 birds.km^{-1}, respectively. The importance of *Donax serra* to oystercatchers on the south and east coasts has been demonstrated in at least one study where oystercatcher densities were strongly and positively correlated with *Donax* biomass (Ward 1990), and in another, much earlier study, where *Donax* was shown to make up 100% of the hard-shelled diet of oystercatchers on sandy beaches (McLachlan *et al.* 1979). While geographic variation in prey densities on sandy shores cannot explain the high proportional increase in oystercatcher numbers over time (there are no data to suggest that the abundance of *Donax serra* has increased concomitantly), the much improved protection status over the years in these areas, coupled with an abundant food supply, is likely to be explain the rapid increase in local populations on sandy beaches along the south and east coasts. Indeed, sandy shores on the south and east coasts now have higher oystercatcher densities (1.89 birds.km^{-1}) relative to mixed shores (1.65 birds.km^{-1})

than was previously the case. In the same areas - densities during the 1979/1980 survey were 1.05 birds.km^{-1} and 0.91 birds.km^{-1}, respectively. It could be argued that food abundance itself has improved for oystercatchers as a result of lower exploitation levels by humans. However, this potential benefit is unlikely to be of significance, because even though oystercatchers rely almost entirely on *Donax serra* on sandy beaches in the Eastern Cape, human exploitation of sand mussels is almost entirely recreational and only accounts for approximately 2% of the standing stock and 7% of the maximum sustainable yield (Schoeman 1996, Sims-Castley & Hosking 2003, Mackenzie 2005).

One further example substantiates the hypothesis that overall increases in oystercatcher numbers on the south and east coasts are explained mostly by the 'release' of populations from high levels of human disturbance in sandy habitats with traditionally high food availability. On a 15 km stretch of coast between the Van Stadens and Gamtoos Rivers numbers have increased from 70 to 296 birds - the greatest single contribution to overall increases in oystercatcher numbers on the south and east coasts. This area contains ideal breeding habitat for oystercatchers and was heavily disturbed by ORVs, which were considered a threat not only to oystercatchers, but also to other coastal breeding birds, such as Damara Terns *Sterna balaenarum* and White-fronted Plovers *Charadrius marginatus* (Watson & Kerley 1995). However, the rapidity with which numbers have increased on this section of coast (and at several other localities for which long-term data exist – Ch. 7) cannot be explained by improved breeding success alone (although it is very likely that breeding success has improved and that this will have additional long-term benefits for local populations). Rather, it would seem that there has been increased settlement of adult birds originating from adjacent areas. In the face of improved habitat quality (e.g. improved food supply or reduced human disturbance), the short-term dynamics of local populations appear to be governed largely by the interaction between nonbreeding, sexually mature birds ('floaters') and locally resident, territorial adults. The reasons for and population-level consequences of these behavioural interactions are explored in Chapters 5 and 7.

On a regional scale, the large increases in oystercatcher numbers on the south and east coasts, and particularly in the east of the breeding range (Vernon 2004), is likely to be responsible for forcing an increase in the easterly movements (in the form of diffusion dispersal) by juveniles outside of the historical breeding range (Hockey *et*

al. 2003, Brown & Hockey 2007). This process also appears to be the most likely explanation for the eastward breeding range extension of oystercatchers that has occurred over the last 25 years. However, it is currently not possible to assess whether the spread of juvenile oystercatchers into Kwazulu-Natal (Brown & Hockey 2007) is simply a consequence of an eastward expansion of the breeding range, or a density-dependent consequence of an increasing density of territorial breeding adults in the east of the range (Vernon 2004). Furthermore, if both the increase in oystercatcher numbers in the east of the range, and the range expansion are current phenomena (as seems likely), it is not clear why they have occurred so recently. Two possible explanations are improved protection in the form of the ORV ban and improved food supply in the east of the oystercatchers' range, due to an eastward spread of *Mytilus*. Yet both these explanations are unsatisfactory.

The ORV ban was only implemented at the end of 2000 - too recently for to explain population increases at a regional scale, because young birds only recruit into the mainland breeding population at approximately 5-6 years of age (Loewenthal 1998, Ch. 5). Similarly, the range expansion cannot be explained by the ORV ban, because birds were already breeding in Kwa-Zulu-Natal before the ban was implemented (Brown & Hockey 2007).

The presence of *Mytilus* is also difficult to invoke as an explanation for population increases in the east of the species' range. Firstly because, on a regional scale, populations have increased on sandy shores in these areas, where *Mytilus* is absent. Secondly, even on mixed shores and rocky shores, *Mytilus* only reached the eastern regions of the Eastern Cape in 2000 (Robinson 2005), well after substantial increases in oystercatcher numbers had occurred (Vernon 2004).

Due to the uncertainty as to the reason(s) for increases in both oystercatcher numbers and range in the east of South Africa, it is difficult to make predictions regarding the species' future population size in KwaZulu-Natal. However, several lines of evidence, not least food availability, suggest that the upper limit to population numbers in this region is likely to be low (Brown & Hockey 2007).

Although the global oystercatcher population has unquestionably increased over the past 25 years, numbers on 41 of 239 stretches of mainland coast (16%) have decreased. Of these areas, approximately 80% have experienced rapid urban development. While these decreases could be explained through lowered breeding success to the point where local populations are no longer sustainable (and

oystercatcher breeding success in many unprotected areas is known to be below sustainable levels – Ch. 6), it is much more likely that breeding birds have moved to adjacent, more favourable habitats, and/or that returning, sexually mature birds have settled in adjacent habitats. Most local decreases were detected along relatively small stretches of coastline (in the order of a few kilometres), and at 72% of the 'decreaser' sites, adjacent populations increased. It is clear that the factors governing population dynamics at a local scale differ from those operating at a regional scale: these aspects are considered in detail in Chapters 5 and 7.

Whatever the reasons for local and habitat-related differences in population trends, the global population size of oystercatchers has increased by *ca* 46% since the early 1980s and now stands at approximately 6670 birds. The regional Red Data Book (Barnes 2000) classifies the African Black Oystercatcher as *Near-threatened* by virtue of the fact that the population size is small (<10 000) and numbers have decreased or were previously recorded as decreasing. By global standards the population is still small (<10 000 birds), but the increase in population size and likely improved breeding performance over the past 25 years (Ch. 3) directly contradict the criteria that precipitated the species' inclusion in regional (Barnes 2000) and international (BirdLife International 2004) Red Data Books. Because the population size remains small, the recent increase in numbers may not be sufficient to warrant the species' delisting. However, there has undoubtedly been a considerable improvement in the species' conservation status over the past two decades, partly as a result of improved coastal conservation measures and partly as a result of increased food supply. Given current trends it may well be possible to propose the species' de-listing in the near future.

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CHAPTER 3

FACTORS AFFECTING THE BREEDING SUCCESS OF THE AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI*

INTRODUCTION

Breeding success among oystercatcher populations worldwide is low (Hartwick 1974, Vermeer *et al.* 1992, Hazlitt & Butler 2001), and largely reflects egg losses, rather than chick mortality (Hockey 1996). Egg mortality in particular is largely due to the ground-nesting habit of the Haematopodidae, which renders exposed eggs vulnerable to a wide range of potential threats, both natural and human related. Of the natural causes of egg loss amongst the world's oystercatchers, natural predators and storms are the most significant (Hockey 1996): this is also true in the case of the African Black Oystercatcher *Haematopus moquini* (Hockey 1983, Jeffery 1987, Jeffery & Scott 2005, Tjørve 2006). Because the intensity of predation and of storms can vary spatially over relatively small scales, as well as temporally, this typically leads to large variation in fledging success amongst the Haematopodidae (Hockey 1996). The mean fledging success across years of a number of American Black Oystercatchers *H. bachmani* populations varied between 0.19-1.1 young.pair^{-1} (Hartwick 1974), while a single population of American Pied Oystercatchers *H. palliatus* produced an average of 0-0.5 young.pair^{-1} over four years (Nol 1989).

In the case of the African Black Oystercatcher, localised studies similarly suggest that variation in breeding success is substantial for the species. At Cape Agulhas in the Western Cape, South Africa, a study of the breeding success of a single population, spanning 20 years, showed a variation in mean annual fledging success of 0-0.81 fledglings.pair^{-1} (Jeffery & Scott 2005), while at Robben Island, South Africa, the average breeding success of oystercatchers between four highly localised populations and over three consecutive seasons varied between 0.13 and 0.86 fledglings.pair^{-1} (Tjørve 2006). Despite egg losses being primarily responsible for breeding failure in the Haematopodidae, chick mortality is also high within the family. Although direct evidence for the causes of chick mortality are difficult to

obtain, most studies suggest that predation is the major cause of chick mortality among oystercatchers (Hockey 1996), with most of this mortality occurring in the first week after hatching (Hockey 1996). In one localised study, mortality of African Black Oystercatcher chicks was 87.5% (Hockey 1983).

Because of the siting and timing of their breeding attempts, African Black Oystercatchers are also vulnerable to the direct and indirect effects of human disturbance (Jeffery 1987, Hockey 1996). Human disturbance can potentially reduce the fledging success of breeding oystercatchers by acting at the incubation stage and/or chick-rearing stage of the oystercatcher breeding cycle, and in different ways.

For example, the first recorded and most dramatic incidence of human disturbance impacting the African Black Oystercatcher resulted from a causeway being built between the mainland and Marcus Island in the Western Cape, South Africa (Cooper *et al.* 1983). The causeway allowed terrestrial mammals onto the island and four species occurred regularly, all of which were predators of birds, their eggs and young. Besides killing adult oystercatchers, over three consecutive seasons between 1979 and 1982, breeding success (fledglings.pair^{-1}.year^{-1}) was lowered by an order of magnitude.

On the mainland coast of South Africa, a variety of forms of human disturbance may also lower the reproductive success of breeding populations. Direct effects of human disturbance have been identified as destruction of nests by walkers and horse-riders, as well as off-road vehicles (ORVs), and predation of chicks by uncontrolled dogs (Jeffery 1987, Hockey & Loewenthal 2002, Jeffery & Scott 2005). Disturbance may also result in drowning of chicks (pers. obs.) and loss of adult foraging time (Lambeck *et al.* 1996), possibly leading to chick starvation (although this probably occurs rarely – Ch. 4).

Potential indirect effects of human disturbance include death of unattended eggs and small chicks through heat exposure (Webb 1987, Adams *et al.* 1999) and possibly through increased predation (Tjørve 2006). Disturbance is likely to increase, because the number of people using the South African coast has increased markedly in recent years (e.g. Watson & Kerley 1995, Prochazka & Kruger 2001).

Despite the threats facing the species, a number of measures have been implemented on the mainland to conserve African Black Oystercatchers, including increased reserve proclamation over recent years (Lombard *et al.* 2004), and, since 2000, a nationwide ORV ban on South African beaches (Department of

Environmental Affairs and Tourism 2003, 2004). Reserve proclamation has significantly benefited oystercatcher populations (Leseberg *et al.* 2000, Ch. 2), and there is good evidence to suggest that an increased food supply, due to the presence of *Mytilus galloprovincialis*, an invasive, alien mussel species, has also been responsible for localised population increases (Hockey & Van Erkom Schurink 1992, Ch. 2). Evidence from this study suggests that improved protection and increased food supply have led to local population increases largely via processes other than increased reproductive success (Ch.2, Ch. 7).

Nonetheless, there are several reasons why both improved protection of coastal areas and increased food availability (in the form of *Mytilus galloprovincialis*) may well also have improved the breeding success of local oystercatcher populations.

Firstly, although oystercatcher populations in protected areas do experience human disturbance, the array and intensity of possible human-related impacts experienced by breeding oystercatchers is likely to be lower than in unprotected areas - particularly for protected sites where monitoring was carried out in this study (see Methods for details).

Secondly, the unique suite of constraints on adult birds when provisioning chicks (Ch. 4) suggests that oystercatchers may be food limited when rearing chicks and that improved food supply and/or protection status may therefore improve the breeding success (in particular the proportion of hatchlings fledged) of local populations. At Malgas Island and Jutten Island in the Western Cape, South Africa, the ratio of one- to two-chick broods increased following the invasion of the shoreline by *Mytilus galloprovincialis* (Hockey & van Erkom Schurink 1992, Ch. 2).

Despite high levels of local and inter-annual variation in reproductive success of oystercatcher populations, studies suggest that populations are benefiting from protection and from an improved food supply due to the invasion of *Mytilus galloprovincialis* (Ch. 2).

Using an extensive nest-monitoring data set covering a large geographic range and spanning many years, the aims of this study were therefore to assess: (1) whether, in spite of large variations in breeding success, protection has improved the reproductive output of local populations; (2) the relative importance of *Mytilus* and protection on oystercatcher breeding success; (3) at which stage of the breeding cycle of the species (e.g. incubation stage, chick-rearing stage) human-related impacts are

having the greatest impact; and (4) exactly what the human-related impacts might be on the reproductive success of African Black Oystercatchers.

METHODS

Study sites and their classification

To assess the factors likely to be most important in influencing oystercatcher breeding success (and given that the potential impacts of human disturbance on oystercatcher populations are central to the study), three approaches were taken.

In the first instance, as an indirect means of gauging the impact of human activity on fledging success, the mean fledging success of unprotected mainland populations (UMPs), protected mainland populations (PMPs) and island populations (IPs) were individually assessed and compared. An oystercatcher population was classified as protected if it fell within a Marine Protected Area (MPA) as defined by Lombard *et al.* (2004), and *vice versa.* A further distinction was made between mainland protected populations and island populations (which also fell within MPAs), with Dassen Island being the only island site for which detailed nest monitoring data were available. All sites thus defined have been protected since the early to mid-1980s.

The rationale for these three population definitions (which were subsequently used in PVA assessments –Ch. 6) is that, despite variation from site to site, there are perceived real differences in human disturbance experienced by oystercatcher populations in these differently defined areas. While human disturbance can be considered negligible on Dassen Island and at Cape Point Breeding Sanctuary (because these sites are closed to the public), there is human activity in other protected mainland areas and the 'protection' afforded by protected areas does thus vary to some extent depending on the level and type of enforcement. Nevertheless, several factors which can potentially affect oystercatcher breeding success in unprotected areas on the mainland which do not operate to the same extent (or at all) in protected areas. These include uncontrolled dogs, high numbers of equestrians, very high densities of anglers, and much higher densities of people in general (e.g. holiday-makers) (Leseberg *et al.* 2000).

Since 2000, there has been a dramatic change in the conservation status of coastal areas in South Africa that fall outside of MPAs in the form of a nation-wide

ORV ban (Department of Environmental Affairs and Tourism 2003, 2004). However, at most unprotected sites, as defined here, there are no quantitative data on ORV presence at coastal sites in this study pre- and post-ORV ban. Furthermore, during the seasons of monitoring after the ORV ban, ORVs were observed at many of the unprotected sites, as has been the case with at least one other extensive study on oystercatcher breeding success (Jeffery & Scott 2005). Thus, the presence or absence of ORVs was not explicitly addressed in this study.

If oystercatcher breeding success is strongly influenced by human disturbance, it was predicted that IPs should have the highest mean fledging success, followed by PMPs, with UMPs having the lowest success rate.

Secondly, because available evidence suggests that the presence of the alien Mediterranean mussel *Mytilus galloprovincialis* may be having a large and positive benefit to oystercatcher populations (Ch. 2), a more detailed analysis was undertaken to examine the relative importance of both *Mytilus* and protection on the fledging success of oystercatcher populations.

Thirdly, an analysis of (a) hatching success and fledging success, (b) age-related mortality of chicks, and (c) causes of egg loss and chick mortality were compared between UMPs, PMPs and IPs, primarily to assess at what stage of the oystercatcher breeding cycle human disturbance might be having the greatest impact – this as a means of narrowing down the variety of important ways in which human disturbance might be lowering oystercatcher reproductive success.

Fledging Success in UMPs, PMPs and IPs

Monitoring data from all sites and years (Fig. 1.1, Table 3.1) were used to compare the fledging success within UMPs, PMPs and IPs. The total number of pairs and number of fledglings for each population were calculated for each season, providing a mean fledging success (fledglings.pair^{-1}.year^{-1}), with the number of monitoring seasons reflecting the sample size for each defined population (in the case of UMPs and PMPs which came from more than one site, sites were also pooled). This gave 57 site-years of data for UMPs, 25 site-years of data for PMPs and 5 site-years of data for IPs (data available only from Dassen Island). Fledging success was compared between the three sites using a one-way ANOVA, followed by Tukey post-hoc tests to assess differences between individual pairs of defined populations.

The influence of *Mytilus* and protection on oystercatcher breeding success

The relative influence of *Mytilus* and protection on oystercatcher breeding success was explored using a general linear model (GLM). The measure of breeding success used was fledglings.pair^{-1}.yr^{-1}, with each data point reflecting the breeding performance of a single pair at a single site in a single year.

Table 3.1: Details of monitoring activities undertaken for populations on islands (IPs), protected mainland populations (PMPs) and unprotected mainland populations (UMPs). De Hoop is listed as both an unprotected and protected mainland site, because its protection status changed significantly during the course of the monitoring period.

Site	Monitoring period	Breeding seasons	Total clutches monitored	Pairs monitored seasonally	Population status
Dassen Island	1998-2003	5	299	39-71	IP
Total (IP)	**1998-2003**	**5**	**299**	**-**	**IP**
Cape Point B.S.	1998-2005	5	100	10-14	PMP
De Hoop N.R.	1986-1990	4	88	16-20	PMP
Goukamma N.R.	1989-2005	16	364	8-17	PMP
Total (PMP)	**1986-2005**	**25**	**593**	**-**	**PMP**
Noordhoek	1997-2005	8	127	9-11	UMP
Soetwater	1999-2005	6	179	10-14	UMP
Betty's Bay	1997-2001	4	47	5-6	UMP
De Hoop	1984-1986	2	41	15-21	UMP
Dana Bay	1999-2002	3	69	12-17	UMP
Gericke's	1996-2005	9	125	7-11	UMP
Brenton-on-Sea	1997-2004	7	39	2-5	UMP
Knysna Lagoon	1997-2005	8	153	9-14	UMP
Keurbooms R.	2000-2003	3	56	7-11	UMP
Kenton-on-Sea	1997-2001	4	70	12-13	UMP
East London	1998-2001	3	91	17-35	UMP
Total (UMP)	**1984-2005**	**57**	**956**	**-**	**UMP**
Grand Total	**1984-2005**	**87**	**1848**	**-**	**-**

Thus, samples for this analysis reflect variation between individual breeding pairs at a site, variation between sites and variation between years. Although nest monitoring has been carried out at all sites and all years given in Table 3.1, not all of these data

were amenable to this analysis, because breeding performance for individual pairs was not always tracked at every site and in every year. Sites were categorized as either being protected or unprotected (see above) and either with or without *Mytilus*. Sites with *Mytilus* present were defined as areas where *Mytilus* covered >40% of all three mussel zones within the rocky intertidal, as outlined by Robinson (2005), while sites with *Mytilus* absent were defined as areas with <5% *Mytilus* in the three zones. At sites lacking details of the status of *Mytilus* (as defined here), this was inferred based on a study by Robinson *et al.* (2005), as outlined in Ch. 2. Based on the limitations of the actual monitoring data, and on whether *Mytilus* status could be defined with confidence, data analysed were restricted to the sites and years listed in Table 3. 2. Based on a combination of *Mytilus* status and protection status, four categories were considered for the purpose of analysis (Fig. 1.1, Table 3.2).

Table 3.2: Details of monitoring data used to assess the relative importance of the mussel *Mytilus galloprovincialis*, and of protection, on the breeding success of oystercatchers. Categories refer to groups of sites defined by the presence or absence of *Mytilus* and of protection.

Site	Category	Years of data	Period	Protection Status	Mytilus Status
Gericke's Point	1	6	1998-2003	unprotected	absent
Dana Bay	1	3	2000-2002	unprotected	absent
Goukamma N.R.	2	13	1989, 1991-2002	protected	absent
De Hoop N.R.	2	4	1986-1990	protected	absent
Noordhoek	3	6	1998-2003	unprotected	present
Soetwater	3	6	1998-2003	unprotected	present
Cape Point	4	4	1998-2003	protected	present
Dassen Island	4	4	1998-2001	protected	present

This analysis did not consider the status of a site as an island or a mainland site *per se*. However, the inclusion of the site at Cape Point, which could be categorized similarly to Dassen Island in terms of *Mytilus* and protection status, provided a degree of assurance that factors specific to Dassen Island (other than those being tested) were not potentially explaining any possible differences in fledging success between categories.

The primary aim of this analysis was to assess whether *Mytilus* and protection significantly influence the breeding success of oystercatchers. However, a full effects model was tested to begin with, incorporating the possible individual effects of year, protection and *Mytilus* status and also the interaction effects of *Mytilus* and year, protection and year and, *Mytilus*, protection and year. Stepwise deletion of firstly non-significant interaction effects and subsequently main effects was carried out to arrive at the minimum adequate model which describes differences in breeding success of oystercatchers between the four different population categories (Table 3.2). Specifically, it was predicted that if *Mytilus* and protection are independently having a positive influence on the breeding success of oystercatcher populations, then:

1. Populations at sites characterised by the presence of both *Mytilus* and protection should have the highest breeding success.

2. Populations at sites characterised by the absence of either *Mytilus* or protection should have equivalent breeding success, if the benefits of high food availability offset the costs of high human disturbance

3. Populations at sites characterized by the absence of both *Mytilus* and protection should have the lowest breeding success.

Based on the categorization in Table 3.2, the observed pattern of breeding success by site category was predicted to be 4>3=2>1.

Causes of breeding failure

A detailed investigation into the causes of breeding failure in African Black Oystercatchers was also undertaken. Because the influence of human activity on oystercatcher breeding success forms an important component of this study, a distinction was again made between island populations (IPs), protected mainland populations (PMPs) and unprotected mainland populations (UMPs - as defined earlier in this chapter) as an indirect means of assessing the manner in which human-related activities contribute to breeding failure in the species. Thus, all analyses were carried out separately for populations in the three defined categories. Analyses involved (a) estimating hatching success (proportion of eggs hatched) and fledging success

(proportion of hatchlings fledged), (b) assessing the pattern of age-related mortality of chicks, and (c) where possible, making a detailed assessment of the actual causes of egg or chick mortality for breeding birds in IPs, PMPs and UMPs.

All monitoring activities were carried out at weekly intervals or more frequently (in most cases nests were checked every three to four days) to minimize the possibility of missing eggs which might have been laid and lost between visits. Although eggs were not always marked or measured, it is highly unlikely that relays were missed because the minimum recorded interval between a lost clutch and a relay for *H. moquini* is approximately 10 days and the mean 22.2 days – Hockey 1983). Based on the data from this study, the minimum recorded interval between a lost clutch and a relay was 12-16 days.

Monitoring activities were initiated each season between October and November and not necessarily at the start of the breeding season. Thus, in a few instances, birds were already incubating eggs when nest monitoring commenced and in a very few cases, some adult birds were already rearing chicks: however, these data were not included in these analyses. It is likely that some egg losses were not recorded because monitoring did not always begin before first clutches were laid. This is likely to increase estimates of hatching success artificially (proportion of eggs hatched). However, because monitoring began early in the breeding season, it is unlikely that this bias was serious. Furthermore, the reason for estimating hatching success was primarily to compare this parameter between the population categories (IPs PMPs and UMPs) and the bias in measuring hatching success is likely to have been consistent across populations.

Once started, nest monitoring continued throughout the breeding season until March/April, by which time breeding adults had either fledged young or had ceased to attempt to breed. The fate of eggs and chicks were tracked over time and where possible an attempt was made to ascertain the cause of egg/chick loss. Given the frequency of monitoring and a robust estimate of incubation time for *H. moquini* (27-39 days, mean 32.1 days – Hockey 1983), in most cases disappearance of eggs between monitoring sessions could be confidently recorded as egg losses. However, there were a few cases (<10% of clutches monitored) where there was uncertainty as to whether eggs had hatched and very young chicks had disappeared, or whether egg disappearance was in fact due to eggs being lost. In these cases, it was assumed that egg disappearances were egg losses. This is likely to reduce estimates of hatching

success artificially (proportion of eggs hatched) and to increase estimates of fledging success (proportion of hatchlings fledged). Again however, the primary reason for estimating hatching success and fledging success was for comparative purposes and it is likely that this bias was also consistent between population categories. Hatching success was therefore calculated as the total number of chicks known to have hatched divided by the total number of eggs known to have been laid, while fledging success was calculated as the total number of chicks known to have fledged divided by the total number of chicks known to have hatched. A Chi-squared analysis was performed to test whether the hatching success (number of chicks hatched) compared with the fledging success (number of hatchlings fledged) were independent of the population category (IP, PMP or UMP).

To estimate chick mortality as a function of age, chicks were divided into four 10-day age classes, namely 0-10 d, 11-20 d, 21-30 d and 31-40d. In most cases, this covered the entire chick-rearing period from hatching to fledging (African Black Oystercatchers in one study fledged at 35-40 d (Hockey 1984), although a more recent study suggests a more variable fledging age of 32-46 d (Tjørve 2006)). Data for this analysis were limited to cases where chicks were first found when they were less than 3 days old. The disappearance of chicks on subsequent visits was then recorded and these records were assigned to the appropriate age-classes. In some instances the chicks disappeared over a time period which also spanned age categories. In these cases, the range of possible ages at which a chick disappeared was calculated and the midpoint of this range was taken as the age at which the chick died.

African Black Oystercatchers display characteristic behaviour when they are rearing chicks and are threatened. These include rodent runs, injury feigning and distraction-lure and threat displays (Hockey 1996): they also give characteristic alarm calls (Baker & Hockey 1984). These behaviours were used to assess the possible presence of chicks in the first instance. Thereafter, the presence of feeding middens and fresh food remains (which often accumulate where adults have been feeding their chicks - Hockey & Underhill 1984) was used to help pinpoint the locality of hiding chicks. Where a chick or chick(s) were known to be present, every effort was made to find them. In cases where two chicks were found in the first instance, but subsequently only one chick was found, the other sibling was assumed to be dead. Because siblings are usually in very close proximity it is unlikely that one chick of a sibling pair was missed during search sessions. In cases where one chick was present

in the first instance, the lack of characteristic adult behaviour on subsequent visits was used to conclude that the chick had disappeared if (as in most cases) no corpse was found, and *vice versa* if the live chick could not be found. In instances where chicks were (a) not found during one or more search session and it was uncertain how many chicks were still alive, or (b) only one or neither of the chicks were found on subsequent visits, these data were not used in age-related mortality analyses, but could be included in analyses of fledging success (proportion of hatchlings fledged). In a very few cases, two chicks were found in the first instance and, although it was clear from adult behaviour that a chick, or chicks were present, they were never observed again: these data were excluded from analyses. A Chi-squared analysis was performed to test whether the age at which chicks died was independent of the population category from which they came (IPs, PMPs or UMPs). Because an initial analysis revealed very low expected frequencies for the deaths of oystercatcher chicks in the 31-40 year-old age class, the data were reanalyzed by pooling the 21-30 year-old and 31-40 year-old age classes (Zar 1996).

During nest-monitoring sessions attempts were made to ascertain the cause of egg loss and chick mortality. In some (rare) cases the cause of egg or chick mortality was observed directly. However, in most instances these events had to be indirectly inferred, for example from shell fragments and/or chick carcasses and spoor of potential predators in the case of predation, or signs of nest flooding in the case of eggs being washed away by high tides. Despite every effort to train less experienced participants, the degree of skill in inferring the cause of egg loss or chick loss from available evidence varied considerably between participants. Based on a thorough examination of the detail of the available data the following categories were considered reasonable for the purposes of assigning a cause to either egg or chick mortality. In the case of egg losses, causes were attributed to: (1) unknown causes, (2) flooding, (3) sand burial, (4) displacement (5) small mammal predation, (6) avian predation, (7) Dogs (feral or domestic), (8) humans, (9) vehicles, (10) abandonment, or (11) other.

Flooding was considered the cause of egg loss if nests which previously had eggs were washed away – whether or not the displaced eggs were found (in quite a few cases, eggs were found intact some distance from a nest that had clearly washed away). Displacement was considered the cause of egg loss where intact eggs were found out of a nest for no obvious reason and were no longer being incubated. Egg

loss was attributed to sand burial where eggs were found partially buried in sand and had been abandoned. In the overwhelming majority of cases, small mammal predation (other than dogs and humans) was attributed to mongoose and/or genet species (based primarily on spoor and/or on the serrated patterning along the edge of shell fragments found at the nest). Based on distribution and habits (Skinner & Smithers 1990), likely mongoose predators are the Large Grey Mongoose *Herpestes ichneumon*, Small Grey Mongoose *Galerella pulverulenta* and Water Mongoose *Atilax paludinosus*, but based on limited records where the predator could be identified to species level, Small Grey Mongoose appears to be the most important small mammal predator (Cape Nature Conservation 2004, Oystercatcher Conservation Programme unpubl. data). Both Small-Spotted Genets *Gennetta genetta* and Large-Spotted Genets *G. tigrina* were also likely predators of oystercatcher eggs (the spoor of the two species is practically indistinguishable). Other mammal predators documented in this study, such as the House Rat *Rattus rattus* (N. Rabie *in litt.*), Brown Rat *R. norvegicus* (G. Crisp *in litt.*), Cape Fox *Vulpes chama* (B. Patterson pers. comm.) , Cape Clawless Otter *Aonyx capensis* (C. Watt *in litt.*, pers. obs.) and Chacma Baboon *Papio ursinus* (U. Pond *in litt.*, pers. obs.) appeared to be very infrequent or only very locally important predators of oystercatcher eggs and were classified under the category "other". Pied Crows *Corvus albus* and particularly Kelp Gulls *Larus dominicanus* appeared to be the predominant avian predators, while White-Necked Ravens *Corvus albicollis* were local predators. Avian predation was inferred based on spoor at the nest and on egg remnants where possible. Predation by domestic dogs *Canus familiaris* was inferred based primarily on dog spoor at nests – shell remnants were rarely found associated with dog spoor. Egg loss was classified as being caused by humans if human tracks were recorded at a nest where eggs were previously present. In some cases it was obvious that the eggs had been crushed by people, but in other cases the eggs were simply gone and it was inferred that these had been removed by humans. These two forms of egg loss were not distinguished in analyses. Vehicles were recorded as the cause of egg loss where tracks went directly over a nest which contained eggs during the previous visitation, whether or not shell remains were found. When eggs were found intact in the nest, but were no longer being incubated, egg loss was attributed to abandonment. Abandonment was inferred based on eggs found intact during at least three visitations coupled with lack of fresh oystercatcher spoor to the nest, lack of characteristic anti-predator behaviour by adults (Hockey 1996) or total absence of

birds in the vicinity of the nest. In some cases, entire clutches were abandoned, but there were also instances where one egg of a (usually) two-egg clutch was abandoned because the other had already hatched and the parent birds had apparently abandoned the remaining egg to take care of the hatched chick: these two forms of egg abandonment were not distinguished. Causes of egg loss were classified as unknown where there was no indication as to the cause of egg loss. The cause of egg loss was also classified as unknown if there were conflicting clues as to the cause of egg loss (e.g. where both dog spoor and human spoor were found at a nest and no other clues were available to infer the direct cause of egg loss).

In the case of chick mortality, causes were attributed to the following categories: (1) unknown causes, (2) drowning, (3) sand burial, (4) mammalian predation (5) avian predation, (6) dogs (feral or domestic), (7) humans, (8) vehicles, (9) abandonment, or (10) other. Invariably, because of the relatively high mobility of oystercatcher chicks, it was usually very difficult to identify the cause of mortality: in most cases these could only be assigned for chicks <1 week old. Chicks were presumed to have drowned if found washed up by the tide but otherwise intact. Corpses often were found at the tide line in amongst debris, presumably where they were less obvious to predators (in some cases nests were flooded while chicks were in the process of hatching or just hatched – and this form of mortality was also classified as drowning). Young chicks (again, often newly hatched) were sometimes found partially buried by sand and dead, but intact: in these cases mortality was assumed to be due to suffocation by windblown sand.

The same suite of mammalian and avian species primarily responsible for oystercatcher egg predation also appeared to be the major natural mammalian contributors to chick predation and similar categories were therefore used. Chick predation (whether by a dog or by small mammal predators or by birds) was inferred where chicks had disappeared and there were signs of a scuffle, particularly excessive numbers of chick down/feathers and associated predator spoor. Humans were classified as the cause of chick mortality where there was a direct link, e.g. evidence of chicks being crushed underfoot. Horse riders frequented some unprotected mainland sites and, where there was evidence of horses having trampled on chicks, this was also classified as human-induced mortality. Chick mortality was classified as being due to abandonment where chicks were found dead but for no obvious reason. In some cases chicks were found either very sick and close to death or fresh corpses

were found where chicks were in very poor body condition. In these situations the causes of mortality were lumped into one category classified as "Other", together with trampling by Cape Cormorants *Phalacrocorax capensis* (recorded in two instances on Dassen Island - J. Visagie *in litt.*) and predation by Great White Pelicans *Pelecanus onocrotalus* (recorded in one instance on Dassen Island - J. Visagie *in litt.*), as well as sibling aggression (observed in at least one instance to have caused the death of a chick - N. Elwell *in litt.*). As with egg losses, the cause of mortality was classified as unknown if no chicks were found and there were no clues, or where there were conflicting clues as to the likely cause of chick mortality. The possibility of starvation as an important cause of chick mortality is addressed in Ch. 4.

RESULTS

Fledging Success in UMPs, PMPs and IPs

Mean and standard deviations for fledging success (fledglings.pair^{-1}.year $^{-1}$) were 0.34±0.24, 0.42±0.19 and 0.91±0.13 for unprotected mainland populations (UMPs), protected mainland populations (PMPs) and island populations (IPs), respectively.

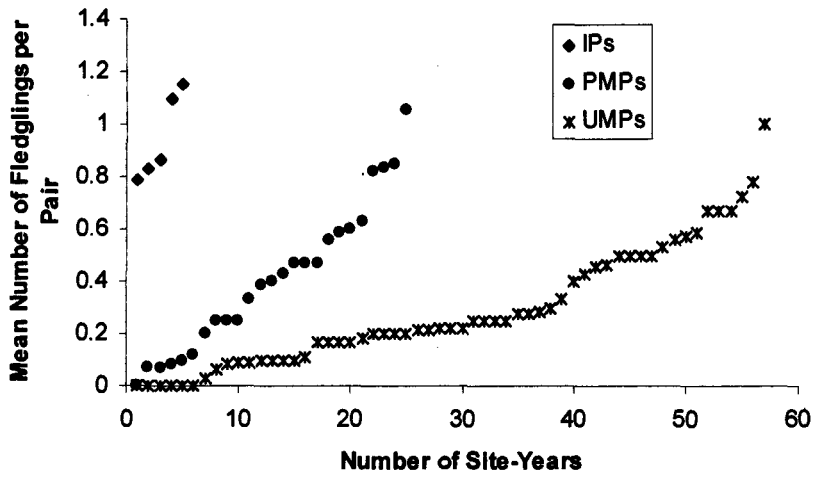

Fig. 3.1: Variation in average breeding success between years and between sites (Table 3.1) for oystercatcher populations in the three population categories - IPs, PMPs and UMPs. Average fledging success is arranged from the lowest to the highest values for each population category.

There were differences in mean fledging success between population categories ($F_{2,84}$ = 17.12, $p<0.001$). Subsequent pairwise comparisons indicated that fledging success

differed very significantly between IPs and UMPs ($q_{3,84} = 8.12$, $p<0.001$) and between IPs and PMPs ($q_{3,84} = 6.30$, $p<0.01$). However, despite large variability in yearly breeding success (Fig. 3.1) there was also a statistically significant difference between PMPs and UMPs, although the significance of this result was less ($q_{3,84} = 3.91$, $p< 0.05$).

The influence of *Mytilus* and protection on oystercatcher breeding success

A series of analyses involving stepwise deletion of non-significant interaction terms and then main effects concluded that there was no effect of year on fledging success and that the effects of *Mytilus* and protection status, and the interaction between *Mytilus* and protection status were consistent across years. However, there was a significant interaction effect between *Mytilus* and protection on fledging success. The minimum adequate model to be tested was therefore one with *Mytilus* and protection status, as well as their interaction, as explanatory variables.

Table 3.3: Fledging success (mean ± SD) for oystercatchers in the four populations defined by *Mytilus* and protection status.

Category	Protection Status	*Mytilus* Status	Fledging success
4	protected	present	0.93 ± 0.28
2	protected	absent	0.37 ± 0.21
1	unprotected	absent	0.32 ± 0.19
3	unprotected	present	0.27 ± 0.13

Given that prior analyses yielded no effect of year, data from all years were incorporated in the model. Using the minimum adequate model and all data (n = 711), there was a significant interaction effect between *Mytilus* and protection on fledging success ($F_{1,707} = 34.93$, $p<0.001$). Given the significance of the interaction effect between *Mytilus* and protection, subsequent analyses to determine whether protection influences breeding success were limited to sites where *Mytilus* was either present or absent. At sites where *Mytilus* was present, the effect of protection was significant ($F_{1,348} = 72.53$, $p<0.001$), but in the absence of *Mytilus*, protection *did not* seem to be a significant influence on fledging success ($F_{1,359} = 0.07$, $p>0.05$). Based on the data and population categories in this analysis, sites with both protection and *Mytilus* had

the highest fledging success, as predicted. The lowest fledging success was expected at sites characterized by being unprotected and lacking *Mytilus*. However, the lowest breeding success was observed at sites which were unprotected and where the mussel was present. Thus, in summary, the expected pattern of differential breeding success relative to the population category was 4>3 = 2>1. The observed pattern, however was 4>2 = 1>3 (Table 3.3).

Causes of Breeding Failure

The fates of 574, 1059 and 1737 eggs were tracked for IPs, PMPs and UMPs respectively. Differences in mean fledging success (fledglings.pair^{-1}.year^{-1}) between IPs and PMPs appear to be largely due to egg losses rather than chick mortality, whereas the difference in mean fledging success between PMPs and UMPs appears to be largely as a result of chick mortality (Fig. 3.2). On Dassen Island, approximately

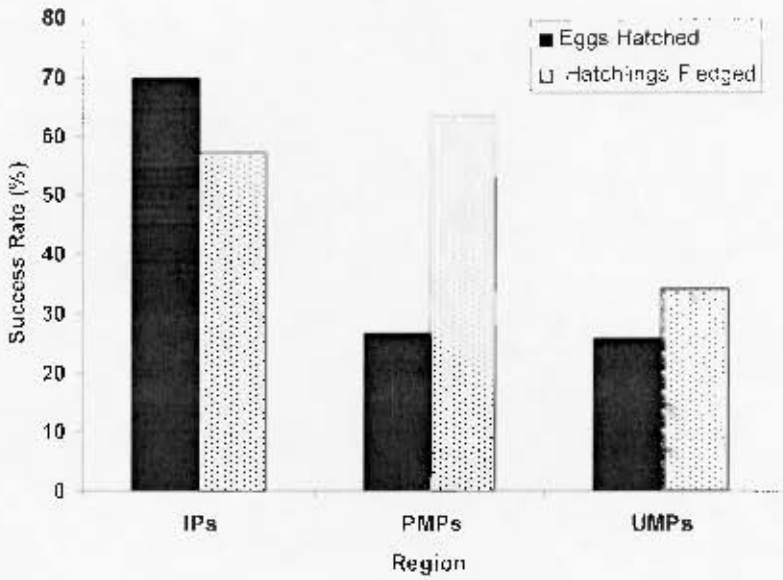

Fig. 3.2: Hatching success (proportion of all eggs hatched) and fledging success (proportion of all hatchlings fledged) for island populations (IPs), protected mainland populations (PMPs) and unprotected mainland populations (UMPs).

70% of all eggs hatched. By contrast, among protected mainland sites, less than 30% of eggs hatched. The proportions of hatchlings fledged at IPs and PMPs were, however, very similar – 57% and 63% respectively. In the case of PMPs and UMPs, hatching success was very similar - 26% and 25% respectively. However, at PMPs

63% of hatchlings fledged successfully, whereas the equivalent figure for UMPs was only 34%. The number of hatchlings compared with the number of fledglings was strongly dependent on whether they came from IPs, PMPs or UMPs ($\chi^2_2 = 25.73$, $p < 0.001$. To assess age-related mortality, the disappearance of 80, 40 and 51 chicks were attributable to an age class for IPs, PMPs and UMPs respectively. In each of the three population categories, the proportion of chicks dying in the first ten days of life (as a percentage of the total chick mortality for each population) was far greater than the proportion dying in any of the other older age-classes (Fig 3.3).

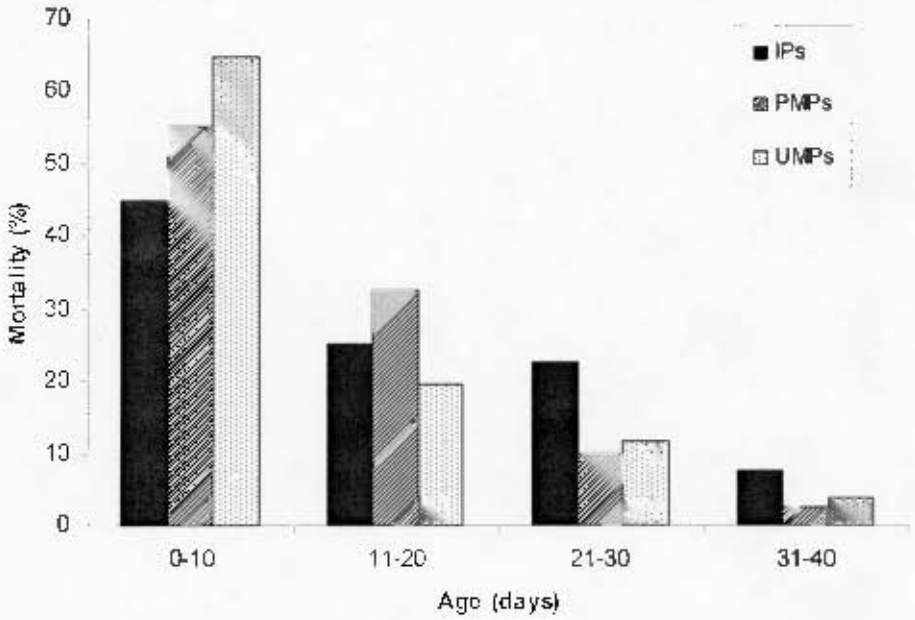

Fig 3.3: Age-related mortality of chicks for island populations (IPs), protected mainland populations (PMPs) and unprotected mainland populations (UMPs). Chick mortality in each age class is expressed as a percentage of the mortality over the entire period, for each of the population categories.

Chick mortalities in the 0-10 day-old age class for UMPs, PMPs and IPs were 66%, 54% and 45% respectively (Fig. 3.3). In general, chick mortality was increasingly skewed towards the younger age classes with a decrease in the level of protection (Fig. 3.3). Statistical analysis confirmed that the age at which chicks died was dependent on the population category from which they came ($\chi^2_4 = 9.85$, $p<0.05$).

Causes of egg losses were based on a total of 574, 1059 and 1737 eggs monitored for IPs, PMPs and UMPs, respectively, but 44-62% of all recorded egg losses were attributed to unknown causes (Fig. 3.4). At Dassen Island, avian predation

(probably mostly by Kelp Gulls *Larus dominicus*) was overwhelmingly the most important of the known causes of egg loss (>60%), followed by displacement (18%) and abandonment (10%) of eggs. At protected mainland sites, mammalian predation (35%), nest flooding (24%) and avian predation (13%) were the three most important causes of egg loss. However, abandonment (12%) and human interference (8%) also

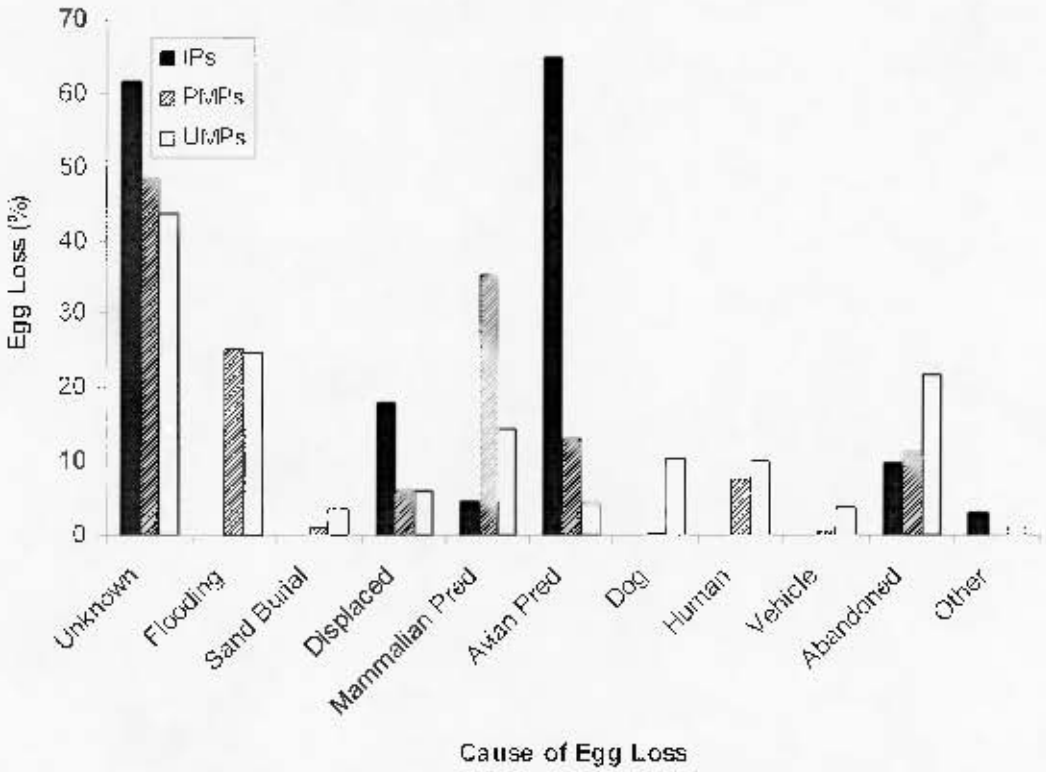

Fig. 3.4: Causes of egg loss for oystercatcher breeding populations on islands (IPs), in protected mainland areas (PMPs) and in unprotected mainland areas (UMPs). Unknown causes are expressed as a percentage of the total number of egg losses, while all other categories are expressed as a percentage of the total known causes of egg loss.

played a measurable role. At unprotected mainland sites, no single factor was identified as being a dominant cause of egg loss. Both flooding (25%) and abandonment (23%) ranked highly, while mammalian predation (14%), dog predation (10%) and human interference (10%) were also important. Causes of chick mortality were based on a total sample size of 401, 279 and 444 chicks monitored for IPs, PMPs and UMPs respectively. However, between 60% and 80% of chick mortality could not be attributed to a cause (Fig. 3.5). At Dassen Island, avian predation (particularly by Kelp Gulls *Larus dominicanus*) accounted for 44% of explicable chick deaths.

However, many chicks (35%) were found dead with no obviously attributable cause (classified as abandoned), while approximately 12% of chicks were either in very poor condition, sick or diseased (making up most of the category "other" – Fig. 3.5). Approximately 7% of chicks appeared to have drowned. In PMPs, the three most

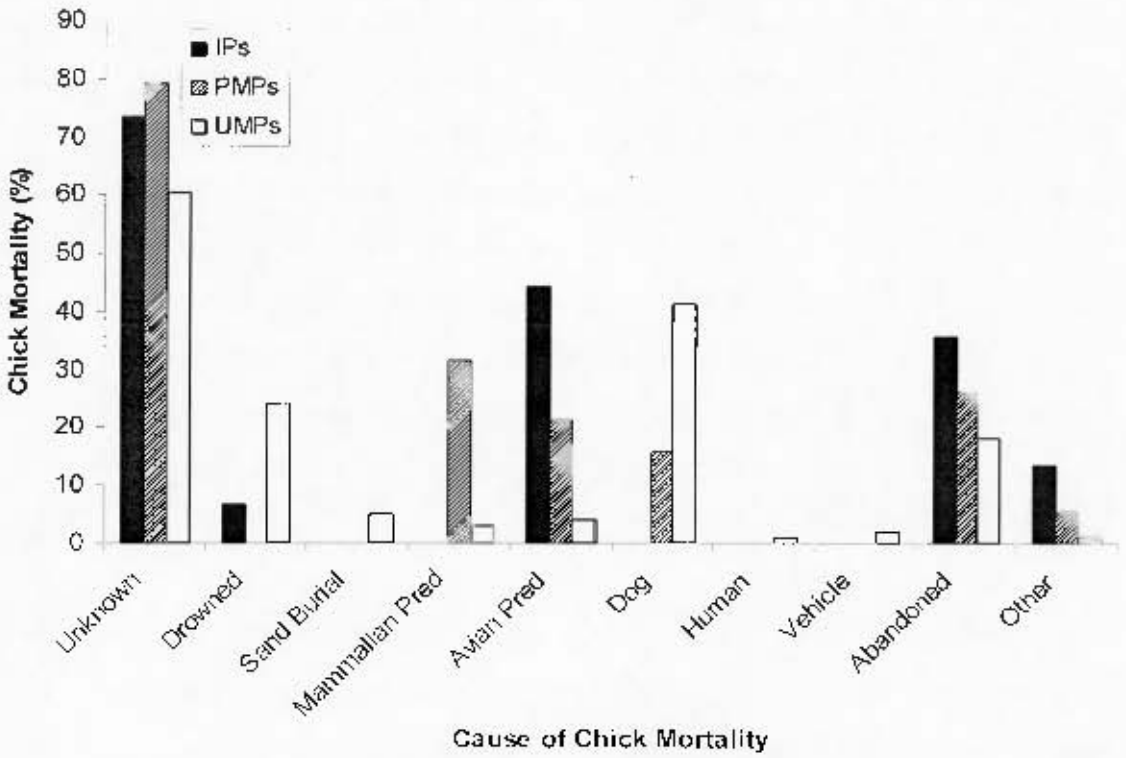

Fig. 3.5: Causes of chick mortality for breeding oystercatcher populations on islands (IPs), within protected mainland areas (PMPs) and in unprotected mainland areas (UMPs). Unknown causes are expressed as a percentage of the total number of mortalities, while all other categories are expressed as a percentage of known causes.

important factors appeared to be mammalian predation (31%), abandonment (27%) and avian predation (22%). However, dog predation (probably mostly by stray dogs) also played a measurable role (16%). In UMPs, predation by dogs stood out as the most important known cause of chick mortality – approximately 41% of all explicable deaths were attributed to this factor. Drowning (24%) also ranked highly, while a relatively large proportion of chicks (18%) were found dead, but for no apparent reason (classified as abandoned).

DISCUSSION

Results of this study confirm the global pattern of low, but variable breeding success among oystercatchers in general (e.g. Hartwick 1974, Baker & Cadman 1980, Nol 1989, Vermeer *et al.* 1992, Schmechel 2001), including African Black Oystercatchers (e.g. Jeffery & Scott 2005, Tjørve 2006). Despite large variability in breeding success within each of the population categories studied, mean annual breeding success (fledglings.pair^{-1}.year^{-1}) across the three population categories differed. This suggests that, despite other factors which may influence breeding success and that may vary within each population category, human disturbance, in whatever form, does lower the breeding success of oystercatcher populations. However, the differences in breeding success between IPs and PMPs was much greater than between PMPs and UMPs. Although PMPs, such as those at Goukamma and De Hoop Nature Reserves, do experience more human disturbance than does the population at Dassen Island, the large difference in reproductive success between IPs and PMPs is probably due more to differences in predation levels (a factor which could not be controlled for in this study), rather than differences in disturbance levels by humans. In most cases, this study confirmed the pattern of high egg mortality which is prevalent among the Haematopodidae (Hockey 1996). Most of the sites in this study (protected and unprotected mainland populations) had low hatching success (Fig. 3.2). In contrast to this pattern, however, birds at Dassen Island had a high hatching success of *ca* 70%, equivalent to that found in Eurasian Oystercatchers *H. ostralegus* breeding on predator-free islands (Harris 1967). Although Kelp Gulls appear to be the most important predators of eggs (and chicks) on Dassen Island, the high hatching and fledging success suggests that their impact on island oystercatcher populations is probably negligible. Although this part of the study focuses on the breeding oystercatcher population at only one island, a study of oystercatcher population trends from two other islands (one lacking breeding Kelp Gulls and another where the Kelp Gull breeding population increased substantially over a 25 year period - Crawford *et al.* in press) indicated that the presence of a gull colony did not appear to limit the growth of the oystercatcher breeding population (Ch. 2). This appears to be contrary to at least one study of Eurasian Oystercatchers where removal of gulls resulted in a large increase in the breeding population (Harris & Wanless 1997).

The low hatching success of eggs at protected mainland sites, relative to islands, and the associated impacts of predatory mammals, strongly suggests that depredation of eggs by natural mammalian predators is the major cause of reduced breeding success at these sites. While terrestrial predators (mainly domestic cats *Felis catus*) are present on Dassen Island (J. Visagie pers. comm.) and feral cats are can have devastating consequences for island bird populations (Nogales *et al.* 2004), they did not appear to be an important source of either egg or chick mortality at Dassen Island. Although most South African islands with breeding populations of oystercatchers are largely free of terrestrial predators, Robben Island in the south-western Cape is a notable exception. Feral cats, snakes (particularly the Mole Snake *Pseudaspis cana*), and House Rats *Rattus rattus* are all potential predators of oystercatcher eggs and/or chicks (Tjørve 2006). Although the oystercatcher breeding population at Robben Island has not obviously experienced reduced breeding success as a result of terrestrial predators (Tjørve 2006), at Marcus Island, a much smaller island, the construction of a causeway which provided access to terrestrial predator species had a very large negative impact on the breeding success of oystercatchers (Cooper *et al.* 1983). Following causeway construction, reproductive success fell to levels apparently equivalent to those of adjacent mainland populations at the time of the study (Hockey 1996). However, given the far more extensive data set from this study, it is likely that the breeding success of oystercatchers on Marcus Island following causeway construction was in fact substantially lower than that of mainland populations in general, at the time. Comparative data on mean fledging success over three breeding seasons from the Marcus Island population (0.03 fledglings.pair^{-1}.year^{-1}-Hockey 1996) and from the mainland populations in this study (0.34 fledglings.pair^{-1}.year^{-1}) indicate an order of magnitude difference in mean fledging success, and highlight the vulnerability of island breeding birds to introduced predators (e.g. Clout & Craig 1995 Courchamp *et al.* 1999, Atkinson 2001, Nogales *et al.* 2004, Blackburn 2005, Wanless *et al.* 2007).

Differences in breeding success between protected and unprotected mainland populations appeared to be due largely to differences in rates of chick mortality rather than egg mortality (although egg mortality was high in both situations - Fig. 3.2). Of the known causes of chick mortality in unprotected areas, it appears that predation by dogs and indirect effects of human disturbance are the most important contributors (Fig. 3.5). In particular, dog predation and drowning ranked highly as contributors to

chick mortality in unprotected, relative to protected, mainland populations: the relatively high incidence of drowning is likely to be as an indirect result of human disturbance. When chicks are potentially threatened, adults utter a characteristic series of calls (Baker & Hockey 1984) to which the chick or chicks respond by lying still, often hiding under rocks, in kelp or among washed up debris. This renders chicks vulnerable to drowning on the incoming tide (e.g. Hockey *et al.* 2000, Hockey & Loewenthal 2002). Because most chick mortality (particularly in unprotected areas) occurs when chicks are very young (Fig. 3.5), the argument for chicks drowning as a result of human disturbance is strengthened. Older chicks can swim well and even dive to evade potential predators (pers. obs.).

Clutch abandonment occurred proportionally more often in unprotected areas than in protected mainland areas or on islands, probably as a consequence of higher levels of human disturbance. Oystercatchers usually lay eggs at 1-2 day intervals (Hockey 1996) and, in cases of asynchronous hatching, eggs that have not yet hatched may be abandoned. This form of abandonment was not distinguished from cases where entire clutches were abandoned. Thus, the apparently greater contribution of abandonment to egg mortality in unprotected areas may be because parents under relatively more stress from human disturbance are abandoning eggs more frequently in favour of the chick that has already hatched. To date, however, no study has explicitly addressed this possibility.

In this study, interactions between factors that may influence hatching and fledging success in African Black Oystercatchers were not addressed. However, more detailed studies suggest that there may be an important interaction between human disturbance (which flushes incubating oystercatchers from the nest) and egg depredation rate (e.g. McGowan 2004). Given that mammalian predation of African Black Oystercatcher eggs is high on the mainland, human disturbance, by repeatedly flushing incubating oystercatchers off the nest may increase parental activity at the nest and hence increase the probability of attracting egg predators. McGowan (2004) established that in a population of American Pied Oystercatchers *H. palliatus*, which experienced very high egg predation rates, there was a negative correlation between nest visitation rates by parental birds and the probability of hatching.

For all population categories, a high proportion of chick mortality was attributable to abandonment (chicks found dead, but with no obvious cause of death - Fig. 3.5). Although, in a few cases, fresh corpses of chicks were found that were

obviously in very poor body condition (presumably due to either starvation, disease or both) such cases were attributed to 'other' causes of chick mortality because in most cases it was not evident why these chicks had died. Overheating and dehydration, particularly among very small chicks, are unsubstantiated possibilities. Most mortality occurred while chicks were very young (Fig. 3.3) when their energetic demands are relatively low, suggesting that starvation is unlikely to be an important cause of human-induced chick mortality. A much more in-depth study of chick starvation as a potentially important form of chick mortality substantiates these findings (Ch. 4).

Although this study did not specifically address the possibility that human disturbance may impact breeding success by forcing breeding birds into marginal habitat, one study has demonstrated that this is an important form of human-induced breeding failure in the American Pied Oystercatcher (George 2002). In this study, there is some evidence from the study site at Noordhoek, Western Cape, that an entire breeding population has been displaced into marginal habitat due to human disturbance. At this site, although breeding adults forage on rocky shores, they do not breed on the sandy beaches backing these prime feeding areas (even though these beaches appear to be 'ideal' breeding habitat). Instead, they breed at an adjacent beach (which has much lower levels of human disturbance), forcing them to fly back and forth over relatively long distances during the chick-rearing period (see also Ch. 2).

In accordance with predictions, breeding populations with both low levels of human disturbance and high *Mytilus* abundance had the highest fledging success. However, contrary to predictions, breeding populations in areas of high *Mytilus* abundance, but with high disturbance levels, had the lowest breeding success. This was contrary to the prediction that the lowest breeding success would be achieved by populations experiencing high levels of human disturbance and lacking *Mytilus*. Indeed, in the absence of *Mytilus*, whether a site was protected or not had no significant impact on breeding success. It is likely that disparities between predictions and observations reflect an inability of the model to control adequately for predation pressure, which is an important factor in explaining differences in breeding success between island and mainland populations. In particular, although populations characterised by the presence of both *Mytilus* and protection included a mainland (Cape Point) and an island site (Dassen Island), the data from Cape Point made up a relatively small proportion (*ca* 7%) of the total number of pair-years for this

population category. Thus, the finding that protection only had a significant impact on breeding success in the presence of *Mytilus* may simply be an artifact of differences in breeding success between island and mainland populations. All populations occurring in areas lacking *Mytilus* were on the mainland and there was no apparent difference in breeding success between these populations, regardless of protection status. Although this suggests that protection may not significantly influence breeding success on the mainland, this particular analysis was limited to far fewer mainland sites and years compared with the initial analysis comparing breeding success between different population categories (i.e. IPs, PMPs and UMPs). Reasons for variation in reproductive success between pairs in African Black Oystercatcher populations is not well understood. However, studies of Eurasian Oystercatchers have identified consistent and large differences in reproductive success between pairs within a single population (Ens *et al.* 1992). In particular, some pairs have high-quality territories where parental birds can feed adjacent to where they breed (termed 'resident' pairs), while other pairs (termed 'leapfrog' pairs) are forced to occupy low-quality territories where the nesting area and breeding area are disjunct. In the case of Eurasian Oystercatchers, it has been found that, in spite of a plentiful food supply, differences in breeding success between leapfrogs and residents are primarily due to the failure of leapfrog parents (who must expend far more time in the transportation of food) to provision their chicks sufficiently (Kersten 1996). Large differences in reproductive success between leapfrogs and resident African Black Oystercatchers within single populations may also explain why, among unprotected mainland populations, *Mytilus* status was not a good predictor of oystercatcher breeding success. In particular, the finding from this study was that (contrary to predictions) unprotected populations characterized by the *absence* of *Mytilus* had a higher breeding success than populations characterised by the presence of the mussel. Unprotected populations characterised by the presence of *Mytilus* in this study, are known to have a high proportion of leapfrog pairs: at Kommetjie approximately 40% of the pairs studied are leapfrogs, while at Noordhoek the entire breeding population has disjunct nesting and feeding areas and some pairs must travel in the region of 500 m between nesting and feeding areas when provisioning chicks (pers. obs.). In comparison, populations at Gericke's Point and at Dana Bay (which are unprotected populations lacking *Mytilus*) have a much lower proportion (*ca* 10%) of leapfrog pairs (J. Sharples, N. Elwell pers. comm.).

While differences in the proportion of leapfrog pairs may explain why unprotected mainland populations characterized by the absence of *Mytilus* had higher breeding success than unprotected populations characterized by its presence, it is difficult to explain putative differences in reproductive success between leapfrog and resident African Black Oystercatchers as being due to chick starvation (as appears to be widespread in the case of Eurasian Oystercatchers – e.g. Ens 1992, Kersten 1996), because chick starvation appears to be an unimportant form of mortality in African Black Oystercatchers (this chapter, Ch. 4). If there are differences in reproductive success between resident and leapfrog pairs of African Black Oystercatcher (as suggested by results of this study), then it would seem more likely that these differences are due to differences in levels of vigilance leading to differential predation rates of eggs and chicks, as has been proposed for both American Pied Oystercatchers (Nol 1989) and European Oystercatchers (Harris 1967, Heppleston 1972, Safriel 1985).

In general, the widespread lack of evidence for chick starvation, independent of whether chicks were reared in areas where *Mytilus* is abundant or not (this chapter, Ch. 4), suggests that starvation is not an important form of chick mortality and that, where it does occur, an improved food supply (in the form of *Mytilus*) is unlikely to decreased its probability of occurrence. Rather, predation levels ultimately determine the fledging success of mainland populations. (In the rare cases where starvation does occur, it is likely to be due to leapfrog birds not being able to transport sufficient food to their chicks).

However, this does not mean that an improved food supply has not improved the chick-rearing ability (and hence fledging success) of African Black Oystercatchers on the South African mainland. Given that terrestrial predators are abundant on the mainland, there may be a strong selection pressure (particularly for parental birds on the mainland) to rear chicks quickly, since, for oystercatchers in general, slow growth and delayed fledging expose chicks to predation risk for longer (Hockey 1996). It has been widely documented that for oystercatchers, the mass, rather than the age of a chick is important in determining when a chick fledges (e.g. Kersten & Brenninkmeijer 1995, Tjørve 2006). For African Black Oystercatchers, as a result of different growth rates, large differences in the time chicks take to fledge (up to 16 days in one instance) have been recorded (Tjørve 2006). In the same study, higher growth rates were linked to an increased probability of birds fledging. Thus, although

starvation appears to be a rare phenomenon among African Black Oystercatcher chicks, an improved food supply may have improved the fledging success of breeding populations on the mainland, by increasing the growth rate of chicks and decreasing the time taken for birds to fledge.

In this study only fledging success, as a measure of reproductive output, was used to assess the possible impact of improved food supply on oystercatcher breeding success. However, there is also some evidence that average clutch sizes may have increased in response to the invasion of *Mytilus galloprovincialis* (despite the fact that studies of other oystercatcher species have found no relationship between clutch size and food availability- Heppleston 1972, Briggs 1984, Safriel 1985, Nol 1989). Among African Black Oystercatchers, the proportion of three-egg clutches among populations (both island and mainland) where *Mytilus galloprovincialis* has become the dominant intertidal bivalve (and prey) has increased over the past 25 years from <0.5% to >5% (Hockey & Loewenthal unpubl. data), this despite the fact that successfully raising three-chick broods to fledging has only ever been recorded twice (Hockey *in litt.*, N. Elwell *in litt*). Sample sizes are still too small to test for the significance of this difference. Given that hatching success is very high on islands (Fig. 3.2), increased clutch size in the absence of high predation levels may explain the rapid increase in brood size (measured as the ratio of one- to two-chick broods) observed on some islands off the west coast of South Africa (Hockey & Van Erkom Schurink 1992).

If the improved food supply has led to an increase in clutch size and/or an increase in chick growth rates, this may explain why, in the absence of *Mytilus*, protection did not significantly improve average fledging success.

All mainland populations experienced much higher levels of predation than island populations. Fledging success is lowest in unprotected sites, where depredation of small chicks by dogs is the primary cause of failure, suggesting that mortality levels caused by uncontrolled dogs are more severe than those resulting from natural predators. Larger average clutch sizes and higher chick growth rates might be crucial in determining whether protection does or does not improve the average fledging success of breeding populations on the mainland. Results from this study and elsewhere (Hockey 1982) indicate that predation events frequently result in only a portion of the clutch or brood being depredated. Thus, larger initial clutch sizes may improve the probability that a pair raises at least one egg or chick to fledging, although this hypothesis has yet to be tested rigorously. At the same time, higher

chick growth rates (due to an abundance of the mussel *Mytilus galloprovincialis*) may have improved the effectiveness of a putative reduction in predation pressure (as a result of protection removing domestic dogs).

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CHAPTER 4

OYSTERCATCHERS AND HUMAN DISTURBANCE: IS CHICK STARVATION FOOD FOR THOUGHT?

INTRODUCTION

Due to the siting and timing of their breeding attempts, African Black Oystercatchers *Haematopus moquini* are vulnerable to the direct and indirect effects of human disturbance (Jeffery 1987, Hockey 1996). In practice it is usually very difficult to determine the precise cause of breeding failure. However, an extensive analysis of nest-monitoring data from areas with little or no conservation protection, compared with those with medium to high conservation protection, have indicated that the effects of human disturbance appear to be having a disproportionately large impact at the chick-rearing stage, rather than the incubation stage (Ch. 3). This is perhaps unsurprising: oystercatchers have a fairly energy-costly mode of chick provisioning involving single-prey loading and mobile Central Place Foraging, a strategy that has been classified as 'precocial 5' (Safriel *et al.* 1996). Furthermore, the foraging of adults is tidally constrained (Hockey and Underhill 1984) and, due to the difficulties in learning the complex techniques involved in foraging, adults are entirely responsible for chick provisioning until well after chicks have fledged (Hockey 1981, 1996). Oystercatchers rear their young during the austral summer (November-March), at the height of the holiday season when human activity and associated disturbance peaks (Hockey 1983a, Leseberg *et al.* 2000). Further, numbers of people using the South African coast have increased in recent years (e.g. Watson & Kerley 1995, Prochazka & Kruger 2001). It has been widely demonstrated that human disturbance can significantly reduce the foraging success of adult oystercatchers (Lambeck *et al.* 1996, FitzPatrick & Bouchez 1998, Coleman *et al.* 2003) and, in the case of the Eurasian Oystercatcher *Haematopus ostralegus*, that experimentally increasing human disturbance of breeding birds reduces the proportion of food allocated to chicks (Verhulst *et al.* 2001).

Taken together, these factors suggest that an important way in which human disturbance may impact on the breeding success of African Black Oystercatchers is through preventing adults from providing offspring with sufficient food.

The entire coastline of South Africa experiences similar tidal regimes (mixed semi-diurnal), but there is a gradient of decreasing intertidal productivity on rocky shores from the Atlantic Ocean coast in the west to the Indian Ocean coast in the south and east (Bustamante *et al.* 1995). A simple time-energy budget model suggests that even in many undisturbed areas, parent birds may struggle to rear two or even one offspring up to fledging, and that these energetic constraints increase with decreasing intertidal productivity (Leseberg *et al.* 2000). However, this model can only predict in which geographical areas oystercatcher chicks have the greatest likelihood of experiencing an energy deficit. What the model does not explore is how this deficit may translate into reduced chick growth - the parameter that has been correlated with survival in Eurasian Oystercatchers (Kersten & Brenninkmeijer 1995).

For African Black Oystercatchers, insufficient data exist which could link reduced growth rates with survival parameters such as fledging probability or post-fledging survival. However, studies of the energetics and growth of Eurasian Oystercatchers have indicated that there is a *critical average growth rate* of approximately 6 $g.day^{-1}$ over the fastest growth period (5-25 d). If chicks grow more slowly than this, the probability of fledging falls dramatically (Kersten & Brenninkmeijer 1995).

Given that a 'benchmark' does exist which links reduced growth to the survival of oystercatcher chicks, it would seem useful to be able to link reduced parental feeding time to its effects on chick growth: this could provide valuable insight into the extent to which human disturbance, in the form of reduced parental feeding time, may affect chick survival.

In this chapter, two approaches are taken to investigate the possible impact of human disturbance on chick growth and, ultimately, chick survival:

1. A model is developed which links parental feeding time to chick growth, the aim of the model being to compare the possible impact of reduced parental feeding time on chick growth between chicks reared in different

regions on the South African coast and assess whether this may have a significant impact on their survival.

2. The body condition of chicks reared under varying disturbance levels (i.e. in protected and unprotected mainland areas and on islands) and between chicks known to have died before fledging as opposed to those that survived to fledging were compared with the aim of assessing whether chick starvation is an important form of human-induced chick mortality.

METHODS

Model development and application

Initial model development

Because of a lack of understanding as to how parent birds partition their feeding time among siblings, the model was restricted to describing a situation where adults rear a single chick. To examine how reduced parental feeding time impacts chick growth for a one-chick brood, a model was developed which describes the growth rate of an oystercatcher chick, based on the supply rate of food to the chick by parent birds and a yield function ($Y(t)$) which describes how the chick converts food eaten into body mass as it grows. In turn, the supply rate of food to the chick was described by the intake rate (K) of adult birds and the increasing time required by parent birds to satisfy both their own energetic demands (Fnb) and that of a single growing chick ($Fb(t)$).

Using the model, it was thus possible to manipulate $Fb(t)$ and examine the impacts of this on chick growth. Because the initial model development described above only considers positive growth of an oystercatcher chick, the model was later modified to allow the chick to enter a negative growth period if the food supply by parent birds was sufficiently reduced (due to a large reduction in $Fb(t)$) such that not even the resting metabolic rate requirements of the chick could be met. A description of the model structure, its development, calibration and underlying assumptions (together with relevant references) are presented as supplementary material to this chapter in Appendix 4.1.

Regional differences in the impact of disturbance on parental foraging time and chick growth

To assess how disturbances to parental foraging time may affect chick growth regionally around the coastline of South Africa, the chick growth model was applied to four areas for which there are data describing available foraging times (*Avf* values) and actual foraging times for non-breeders (*Fnb* values) in minimally disturbed areas (Leseberg *et al.* 2000). These are Marcus Island in the West Coast National Park (33°02′S, 17°58′E); De Mond sanctuary within the Cape of Good Hope Nature Reserve (34°15′S, 18°23′E) on the Atlantic seaboard; and De Hoop (34°29′S, 20°30′E) and Goukamma Nature Reserves (34°04′S, 22°50′E) on the Indian Ocean coast. Available foraging times come from Leseberg *et al.* (2000) and represent the potential foraging time available to oystercatchers over each tidal cycle (Fig. 1.1).

Although manipulating *Fb(t)* is useful in gaining an understanding of the chick growth model, in the context of simulating disturbances to parental foraging time, it was desirable to express this in terms of a reduction in available foraging time rather than as a reduction in *Fb(t)*, because a disturbance experienced by provisioning parents will not necessarily impact on chick growth - i.e. there is a foraging time 'buffer space' which has to be exceeded before there is any energetic impact on a growing chick.

Because this buffer space varies regionally (Leseberg *et al.* 2000), there are regional differences in the amount of available foraging time parent birds could lose before chick growth is even impacted. Thus, ultimately, the impact of perturbations to chick growth will vary regionally: it was this variation in the impact on chick growth that was of particular interest in the study. The model was therefore altered so that any simulated disturbance to parental foraging time could be expressed in terms of *Avf*.

The manner in which reductions to available foraging time and their impacts on chick growth were modelled are incorporated in Fig. 4.1. As an example (Fig. 4.1), a constant perturbation is applied, reducing the available foraging time to an arbitrary level *Pf*, representing the amount of available foraging time left to parental birds.

Reducing *Avf* to a level X, does not affect the growth of the chick (irrespective of the age of the chick) because the disturbance does not impinge on *Fb(t)*. However, disturbances in excess of this do affect chick growth, because *Fb(t)* itself is reduced.

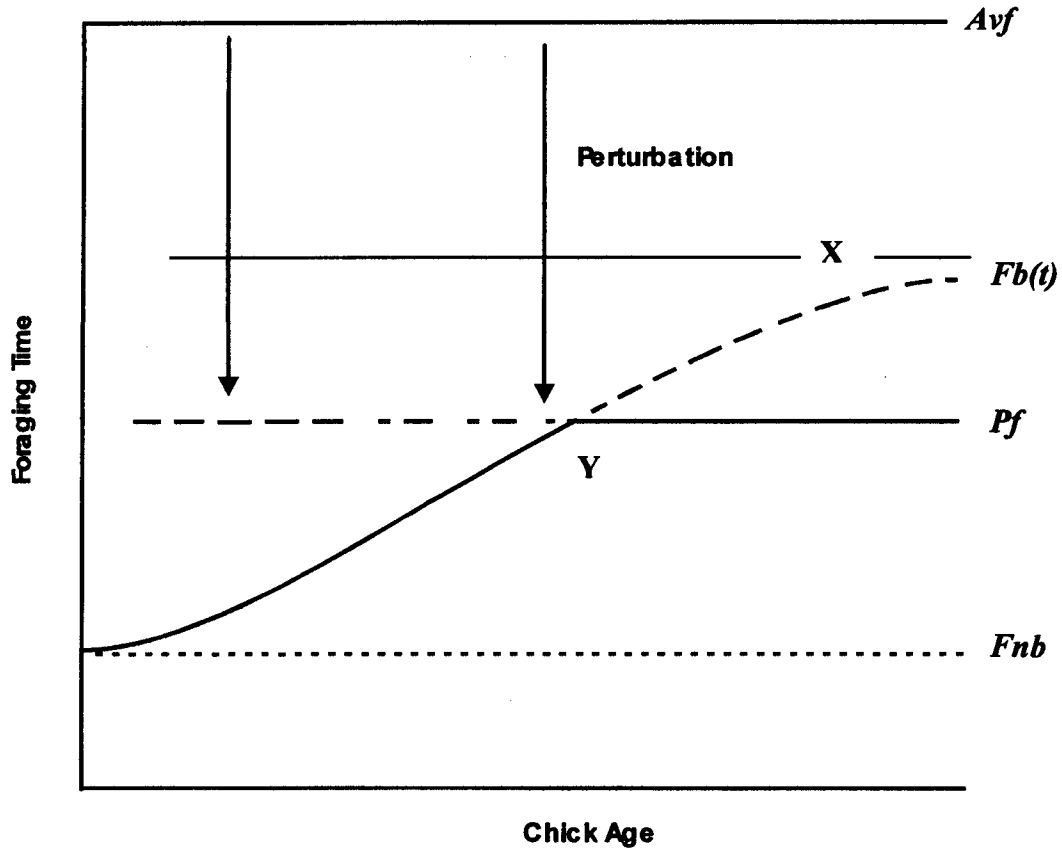

Fig. 4.1. Schematic diagram illustrating how disturbance to parental foraging time was modelled. *Avf* = available foraging time, *Fb(t)* = parental foraging time as a function of chick age, *Pf* = the amount of available foraging time left to parental birds that have been disturbed. *Fnb* = foraging time of a non-breeding adult. The line X represents the level to which *Avf* can be reduced without impinging on *Fb(t)*, and hence chick growth, for any chick up to 37 days old. Reducing *Avf* to a level *Pf* results in chick growth being impacted, but only for chicks older than age Y in the figure.

In this example, reducing *Avf* to a level *Pf* results in the chick growing without any constraint on food supply (i.e. following the growth curve of a chick fed *ad lib*) (hereafter termed an 'ideal' chick - see also Appendix 1) up until age Y because *Fb(t)* is not affected. However for any chick older than age Y, growth will be curtailed because parental foraging time *Fb(t)* is impinged upon (Fig. 4.1). In the hypothetical example given in Fig. 4.1, a reduction in available foraging time is applied over the entire chick growth period and for both low-tide cycles daily. However, for each region, a disturbance regime simulating only weekend disturbances to parental foraging time was also applied. An example of how weekend disturbances to parental foraging time were modelled, as well as the resultant affect on chick growth is given in Figs. 4.2a and b. In the case of a weekend disturbance regime, the way in which

weekends are spread over the growth period of the chick, will change the way in which the growth of the chick is impacted. A weekend disturbance regime was therefore defined as one where disturbances were implemented from the end of the first week of the chick's life, and for every subsequent weekend during the chick's growth period.

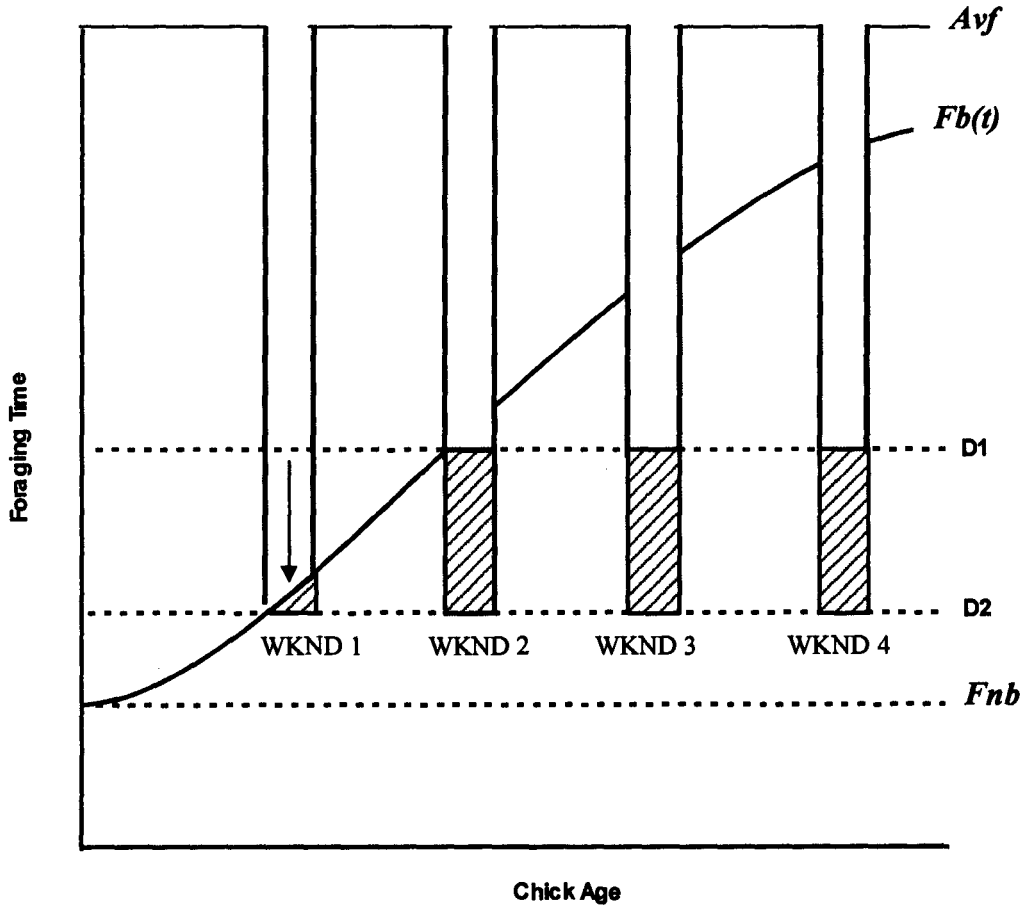

Fig. 4.2a. Schematic diagram illustrating how *Avf* can be reduced in the model to simulate a weekend disturbance regime. In this case, *Avf* is reduced first to a fixed level, D1, and then further to level D2 for two days per week, simulating a situation where parental feeding time is curtailed only over weekends (WKND). In this case, the simulation is such that the growth period of the chick covers four weekends, and hence four such disturbance events. In the case of the series of weekend disturbances D1, over the first weekend the growth of a single chick is not affected, because *Fb(t)* is not reduced –i.e. there is still surplus foraging time available to adult birds after satisfying their own energetic demands and that of a single chick. The arrow in the diagram illustrates the amount of foraging time that parental birds rearing a single chick could still theoretically lose, without the growth of the chick being affected, at this stage of its life. For all other weekends, the series of disturbances D1 and D2 reduce the required parental foraging time (*Fb(t)*) and hence affect the growth of a single chick by varying degrees. The resultant effect on the growth of a single chick in each case is shown in Fig. 4.2b.

Thus, in the model, available foraging time to parent birds was reduced over four weekends during the chick's growth period (Fig. 4.2a – The model could only be calibrated for the growth of a chick between 1 and 37 days old – see Appendix 1). Perturbations to the available foraging time of parent birds were carried out over both low-tide periods and for each day of the weekend. In all cases it was assumed that parent birds used up available foraging time to satisfy their own energetic requirements before those of the chick. A further important assumption of the model is that a chick of a particular age cannot grow faster than an equivalent 'ideal' chick of the same age over the simulated growth period.

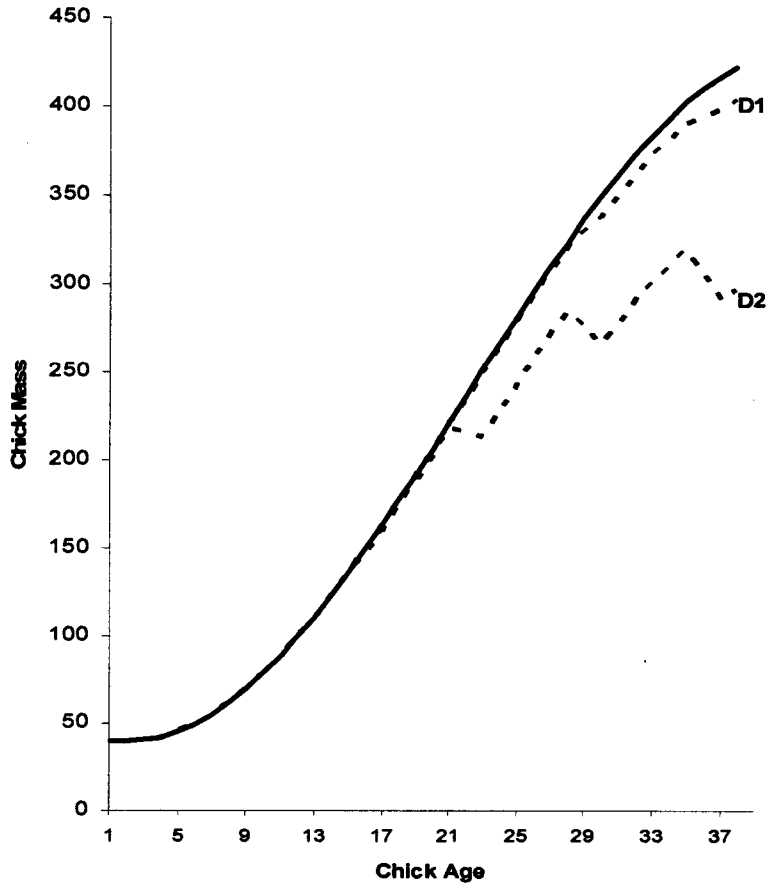

Fig 4.2b. Growth curves for two single chicks whose parents experience disturbance regimes D1 and D2 (Fig. 4.2a). Note that disturbance regime D1 simply slows the growth of the chick whereas with D2, the chick loses weight, because reductions to parental foraging time result in chick not receiving enough food to satisfy even its resting metabolic rate (*RMR*) requirements (see Appendix 1). In each case, D1 and D2 represent a series of weekend disturbances which reduce parental foraging time (Fig. 4.2a). The solid line represents the growth of a single 'ideal' chick whose parents are not subject to a reduction in foraging time.

This assumption is highlighted in the example given in Fig. 4.2b, where, following periods of negative growth the increase in the mass of a chick does not allow it to fully 'recover' (i.e. once again attain a mass that is equal to that of an 'ideal' chick of the same age).

To apply the model to the four regions, it was assumed that the *Y(t)* function derived in the baseline model (Appendix 1) remains unchanged. This seems reasonable because *Y(t)* reflects the physiological characteristics of a healthy, growing chick – a factor unlikely to vary significantly in a regional context. Intake rates (*K*) were calculated by using Nagy's (1987) predicted value based on body mass for the daily energy intake of an adult oystercatcher (996 kJ) and the average foraging times per low tide cycle for non-breeding birds (*Fnb*) in each area (Leseberg *et al.* 2000, Hockey 1984b). To convert foraging times and available feeding times from minutes per low water period (Leseberg *et al.* 2000) to minutes per day (24 hours) values were simply doubled – hence, in the model, no variation in these parameters is incorporated. *Fnb* values, *Avf* and *K* values thus derived are given in Table 4.1.

Table 4.1. Input values used for regional simulation models of chick growth. Values for available foraging time (*Avf*) and non-breeder foraging time (*Fnb*) come from Leseberg *et al.* (2000). See text for derivation of *K*-values.

Region	*K*-values (kJ.min^{-1})	*Avf* (min.day^{-1})	*Fnb* (min.day^{-1})
Marcus Island	3.86	716	258
Cape of Good Hope N.R	3.43	720	290
De Hoop N.R.	2.34	642	426
Goukamma N.R.	1.82	900	546

All values used in the model were expressed in terms of grams wet mass (assuming an 85% water content and a food energy value of 20kJ.g^{-1} dry mass – see Appendix 1) and days. Manipulating Eq. 4.3 (see Appendix 1) and using calculated *K* and *Fnb* values for the different regions, it was possible to generate *Fb(t)* curves for each area, which represent, for each area, the increase in foraging time of parental birds required to satisfy the energy requirements of an 'ideal' chick as it grows (Fig. 4.3).

Using these models, a series of simulations were carried out where the available parental feeding time (*Avf*) for each region was reduced to a) simulate a weekend disturbance regime and b) simulate a continuous disturbance regime.

In the case of both a weekend disturbance regime and a continuous disturbance regime, the total available foraging time to parent birds in each region was systematically reduced and the effects of these perturbations on chick growth were measured as the difference in mass at the end of the simulated growth period (37d) between a chick following the 'ideal' growth curve (Appendix 4.1) and one whose growth is impacted by disturbance (from here on in this difference is referred to as the 'mass deficit').

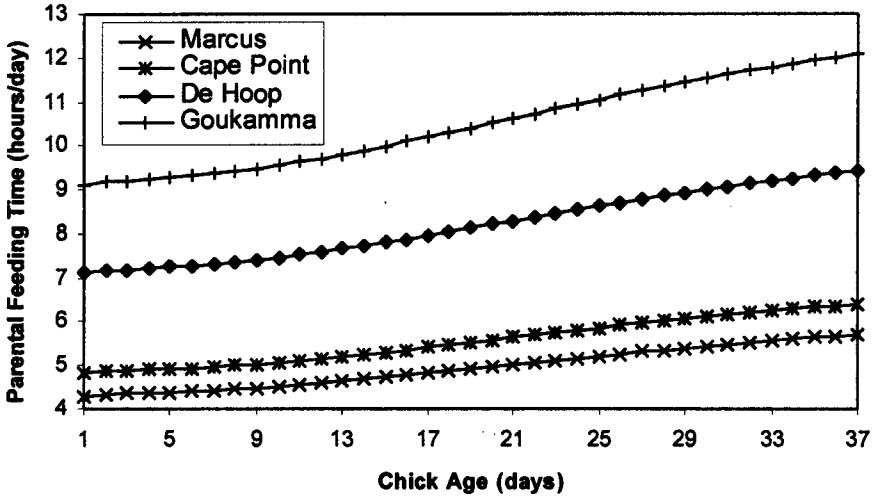

Fig. 4.3. Model-generated curves showing the increase in foraging time required by parental birds (*Fb(t)*) in four different regions, in order to satisfy both their own energy requirements and that of a chick following the growth pattern of an 'ideal' chick (see Fig. 4.2b).

Chick condition and disturbance levels

To test the hypothesis that chick body condition is linked to disturbance levels, three breeding situations were considered: (1) Unprotected Mainland Areas (the East London, Port Elizabeth and Garden Route environs on the south coast of South Africa, the Cape Peninsula (western seaboard) and Cape West Coast; (2) Protected Mainland Areas (Goukamma and De Hoop Nature Reserves on the south coast of South Africa, and De Mond sanctuary on the western seaboard of Cape of Good Hope Nature Reserve); and (3) Islands (Dassen Island, and Jutten and Malgas Islands in

Saldanha Bay). Testing the hypothesis rests on the assumption that the areas outlined here do in fact represent areas of varying levels of human disturbance. Certainly this holds true for island sites, as opposed to all mainland sites. The islands considered here have all been protected as Marine Reserves since the late 1970s or early 1980s (Hockey 1983b) - human disturbance is thus minimal at these sites. Protected mainland sites considered here (Goukamma N.R. and De Hoop N.R. in particular) do experience relatively high visitation rates, but are unlikely to be as heavily disturbed as the unprotected sites considered here (Leseberg *et al.* 2000). All unprotected areas from which data were collected were from popular coastal areas within 10 km of coastal towns or major metropolitan areas.

The alien invasive Mediterranean Mussel *Mytilus galloprovincialis* continues to spread around the coastline of South Africa (Robinson 2005), has increased significantly on west coast islands (Hockey & Van Erkom Schurink 1992) and appears to have benefited oystercatchers (Chapters 2 and 3). It would therefore have been useful to have considered the presence or absence of *Mytilus* as an additional factor possibly influencing chick body condition. However, limited data from mainland protected sites was available – trying to tease apart the possible effects of *Mytilus* and protection would have resulted in a paucity of data from protected mainland sites with *Mytilus* present. Most of the analyses were therefore limited to considering only protection status (as a surrogate for human disturbance) and its possible impact on chick body condition. However, for two sites – Malgas Island and Jutten Island in Saldanha Bay, it was possible to compare chick body condition before (1979-1982) and after (1997-2003) the *Mytilus* invasion. Because protection status has not changed between these periods it was hypothesised that any difference in chick body condition could be attributed solely to the presence of *Mytilus*. On these same islands, both increases in breeding success and increases in population numbers can be attributed to the *Mytilus* invasion (Ch. 2).

To test the hypothesis that chicks in good condition are more likely to survive than those in poor condition, body conditions of chicks known to have fledged were compared with body conditions of chicks known to have died before fledging.

In each of the defined areas (Unprotected Mainland, Protected Mainland and Islands), single point, morphometric data from chicks ≥2 weeks old were used as a measure of body condition. Data come from measurements of chicks ringed in these areas between 1997 and 2003. The measure of body condition used here was body

weight, standardized for body size by tarsal length (i.e. mass to tarsal length ratios). Although tarsal length measurements of adult Eurasian Oystercatchers *Haematopus ostralegus* have been shown to have relatively poor repeatability between observers (Durell *et al.* 2001), and wing length is widely considered to be a reliable surrogate for structural size in several bird species (Ward 1969, Mascher & Marcström 1976, Owen & Cook 1977, Pienkowski *et al.* 1979, Davidson 1983, Gosler 1998) including Oystercatchers (Zwarts 1996), tarsal length was used here because it is the most conservative growth parameter for African Black Oystercatcher chicks (Hockey 1984a). Due to the mathematics of scaling, Kotiaho (1999) points out that both the linear parameter (in this case tarsal length) and the volumetric measure (in this case, body mass) should be log transformed (although in at least one case, leaving the linear parameter untransformed had no effect on the conclusions of the study (Marshall *et al.* 1999)). The same procedure was followed here, with both tarsal length and body mass being log transformed, and it was then assumed that the relationship between the two parameters was linear. Although linear regression equations fitted the data well – see Results – it should still be noted that analyses of body condition assume an underlying linear relationship between the two parameters. Even after data transformations, this assumption may not necessarily hold (Green 2001).

Either the slopes or elevations of the resultant regression equations were used to compare:

a) the body condition of chicks between the three defined areas,

b) differences in body condition of chicks on the Saldanha Bay islands pre- and post-*Mytilus* invasion, and

c) differences in body condition between chicks known to have fledged and those that died.

All chicks included in these analyses were individually colour ringed (at the time of measuring), such that birds known to have fledged successfully could be matched with the morphometric measurements taken while they were still chicks. Chicks were considered to have died before fledging if they were not seen after at least three visits (spanning approximately 3 weeks) subsequent to being ringed. If neither the presence

of *Mytilus* nor human disturbance influences chick body condition, and body condition does not affect chick mortality rates, it was predicted that:

1. Body condition should not differ in response to either the level of protection or the presence or absence of *Mytilus*.

2. Within sites, body condition of chicks should not differ pre- and post-*Mytilus* invasion.

3. Birds that fledged successfully should have been in no better body condition as chicks than those birds that died before fledging.

Comparisons (above) did not distinguish between one- chick broods and two-chick broods, yet a simple energetics model suggests that oystercatchers may struggle to rear two chicks to fledging, particularly in the east of the breeding range (Leseberg et al. 2000). Studies of American Black Oystercatchers *H. bachmani* (Groves 1984) and Eurasian Oystercatchers (Safriel 1981, Ens *et al.* 1992, Kersten 1996) indicate that a sibling hierarchy is established and that as a consequence, the subordinate chick within a brood frequently dies due to competition for food. If adult prey delivery rates to African Black Oystercatcher chicks are significantly impacted by human disturbance, it was expected that there may be large differences in body condition between chicks in one- and two-chick broods. Additionally, if sibling hierarchies are established in the face of severe food competition, it was expected that there may also be large and widespread differences in body condition between first- and second-born chicks within a two-chick brood. An additional set of analyses were therefore undertaken to assess whether there are consistent differences in body condition between:

a) first- and second-hatched chicks within two-chick broods, and

b) chicks from one-chick broods as opposed to chicks from two-chick broods.

For both comparisons a) and b) above, only chicks old enough to be colour ringed (≥2 weeks) and from nest-monitoring study sites were used. At these sites, the fates of

eggs and chicks were tracked at weekly or more frequent intervals over several breeding seasons (refer to Ch. 3 for details).

For comparison a) above, for many broods it was possible to identify first- and second- born chicks based on actual observation of the hatching sequence. These individuals were colour marked (and subsequently colour ringed). Comparisons were only made for chicks from mainland areas and from islands - there were insufficient data to make separate comparisons for chicks in protected and unprotected mainland areas. However, it was predicted that if starvation is a widespread cause of human-induced chick mortality, then differences in body condition between first-and second-born chicks should be more pronounced on the mainland than on islands, because all mainland breeding populations are subject to far higher levels of human disturbance than are island populations.

For comparison b) above, chicks from one-chick broods were identified as chicks with no siblings after the first week since hatching and *vice-versa* for the identification of two-chick broods. Comparisons of body condition were made for chicks reared in protected mainland areas, unprotected mainland areas and on islands.

RESULTS

Regional differences in the impact of disturbances on parental foraging time and chick growth

Results from regional simulations indicated a clear and common trend in terms of the way in which the proportional chick mass deficit at the end of the chick-rearing period increased with increasing perturbation time.

Initially the effect of increased perturbation time on the mass deficit was only marginal. However, at some point for each region (hereafter termed the 'threshold'), any further increase in the perturbation time resulted in an exponential increase in the mass deficit (Fig. 4.4). (In all cases, results are only plotted from the point at which perturbations begin to impact on chick growth. The latter varies substantially between regions and essentially reflects the difference in buffer space between *Avf* and *Fb(t)*max during the growth period (see also Figs. 4.1, 4.2a, 4.3)). Model results suggest that in the case of a weekend disturbance regime a mass deficit would first become apparent when the available feeding time of adults is reduced by *ca* 56%,48%,16% and 20% at Marcus Island (MI), Cape Point N.R.(CPNR), De Hoop

N.R.(DHNR) and Goukamma N.R. (GKNR) respectively. Applying a continual disturbance regime would result in similar or only marginally different values in this

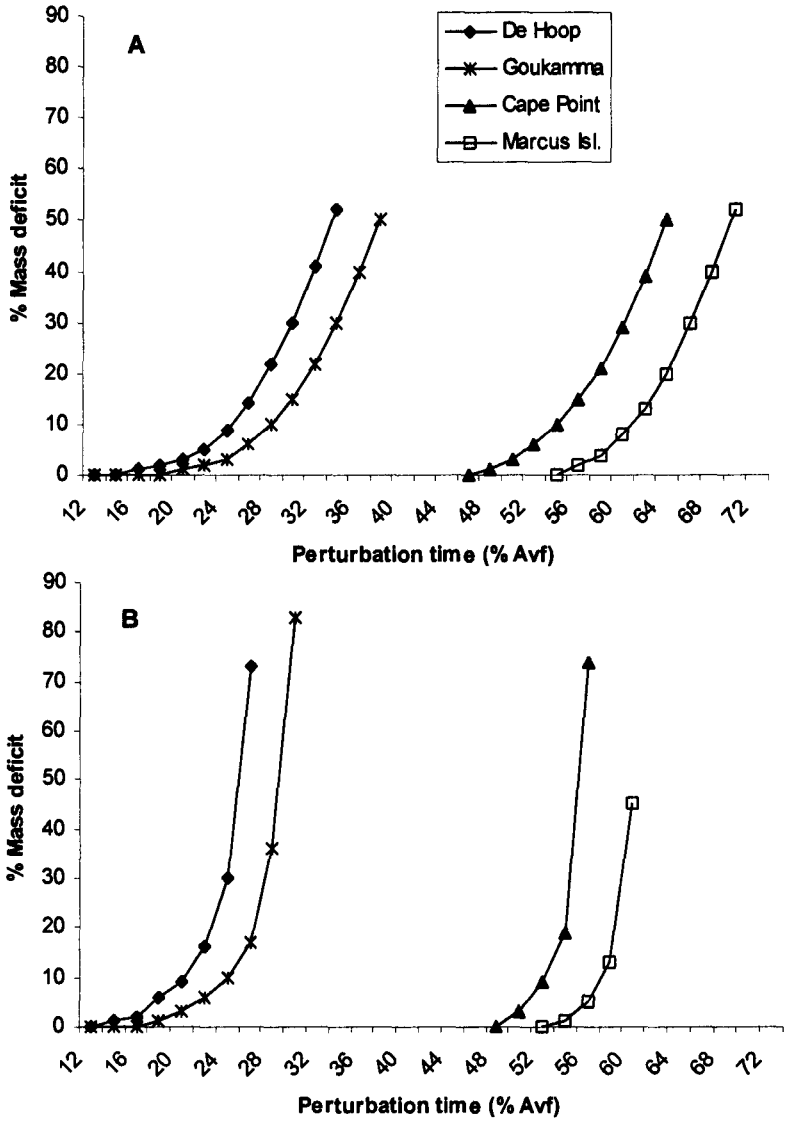

Fig. 4.4. Series of curves showing the effect of A: a weekend disturbance regime (for every weekend from the time a chick is one week old); and B: a continual disturbance regime on the growth of an oystercatcher chick at four different sites. Each point represents the result of one simulation covering the growth period from 1 to 37 days. Percentage mass deficit refers to the difference in mass at 37 days between a chick whose parents experience no disturbance and one whose parents experienced a varying level of disturbance, expressed here as loss of a percentage of their available feeding time (%*Avf*).

respect - 52%, 48%, 12% and 16% for MI, CPNR, DHNR and GKNR respectively. The reason for this similarity in the point at which a mass deficit *begins* to become apparent, is based on the way in which the weekend disturbance regime was spread

over the growth period of the chick. Clearly, in the case of a continual disturbance regime, the oldest chicks with the highest energy demands will always be affected first as available foraging time of parent birds is progressively reduced (see Fig. 4.1). However, in the case of a weekend disturbance regime as modelled here - one of the weekends over the chick growth period corresponded very closely to the period during which chick energetic demands (and hence required parental foraging time, *Fb(t)*) were maximal (Fig. 4.2a). Thus, a progressive reduction in foraging time over weekends, resulted in a similar point at which a mass deficit *began* to become apparent, because both for a weekend disturbance scenario and a continual disturbance scenario, the oldest chicks with the highest energy demands were impacted first.

Predictably, however, further reductions in available foraging time (beyond the point at which a mass deficit became apparent) had a much more severe impact on chick growth in the case of a continual disturbance regime as opposed to a weekend disturbance regime. Specifically, the threshold in mass deficit was much more clearly defined in the case of a continual disturbance regime (Fig. 4.4). Thus, any further reduction in available foraging time beyond the threshold resulted in a much more rapid increase in the mass deficit in the case of a continual disturbance regime (Fig. 4.4). Comparing the total amount of available foraging time that would have to be lost to induce a 50% mass deficit (i.e. resulting in a chick mass of half that for an 'ideal' chick at the end of the growth period), provides a useful way of highlighting the difference in impact on chick growth of a continual as opposed to a weekend disturbance regime for single-chick broods reared in the different regions.

For single-chick broods reared at De Hoop, parent birds could sacrifice *ca* 34% of the total available foraging time over weekends before a mass deficit of 50% was induced over the chick growth period. However, at the same site, only 24% of the available foraging time could be sacrificed on a daily basis before chick growth was impacted to the same extent. For chicks reared at Goukamma, the corrosponding figures were *ca* 40% and *ca* 28%, respectively (Table 4.2).

At Marcus Island and Cape Point, far more foraging time could be sacrificed to disturbance (either over weekends or continually) before a 50% mass deficit was induced, due primarily to the large amount of surplus foraging time available (Table 4.1). At Marcus Island, parent birds could theoretically sacrifice *ca* 70% of available foraging time to disturbance over weekends before single-chick broods were impacted

at the 50% level, while *ca* 54% of available foraging time could be sacrificed daily before the same mass deficit was induced. Corresponding figures for Cape Point were *ca* 64% and *ca* 54%, respectively (Table 4.2).

Table 4.2. Summary of results for regional chick growth *vs* disturbance simulation models. Values indicated are the perturbation times (expressed as percentages of available feeding times for each region) which parental birds could theoretically sacrifice to disturbance before 'ideal' chick mass is halved at the end of the simulated growth period (see text). C.D. = Continual Disturbance, W.D.= Weekend Disturbance

	Marcus Is.	Cape Point N.R.	De Hoop N.R.	Goukamma N.R.
C.D.	54	54	24	28
W.D.	70	64	34	40

Comparisons of body condition

There was a significant difference between the three slopes of mass regressed against tarsal length for chicks from Protected Mainland Areas, Unprotected Mainland Areas

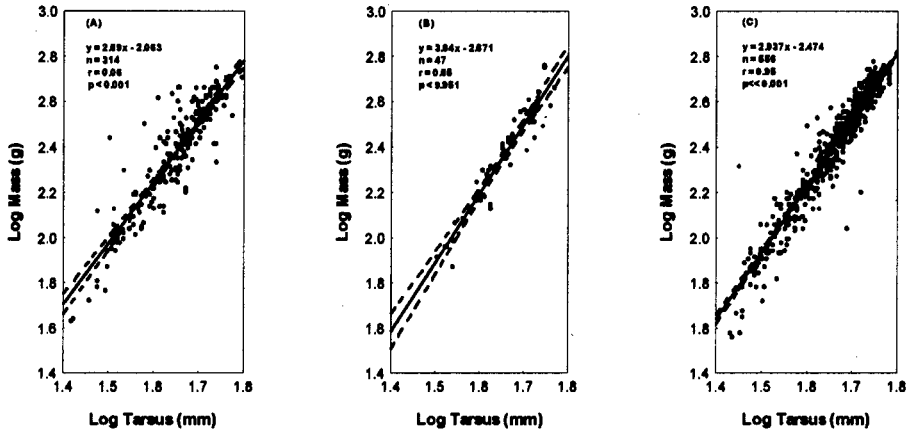

Fig. 4.5. Body condition (log mass/log tarsus) of oystercatcher chicks reared in (A) Unprotected Mainland Areas (B) in Protected Mainland Areas and (C) on west coast islands.

and Islands ($F_{2,811}$ = 4.67, $p<0.05$) (Fig. 4.5), suggesting that chicks from the three different treatments do differ in body condition. Post-hoc testing (Tukey test), however, revealed no difference in body condition between chicks from Protected and

Unprotected Mainland Areas ($q_{3,257}$ = 2.63, p>0.05) nor between Protected Mainland Areas and Islands ($q_{2,601}$ = 0.81, p>0.05). Overall differences in chick body condition were thus entirely attributable to differences between chicks in Unprotected Mainland Sites and on Islands ($q_{2,776}$ = 4.1, p<0.05). Visual inspection of the data indicate that variability in body condition was greatest for chicks from unprotected mainland areas (Fig. 4.5).

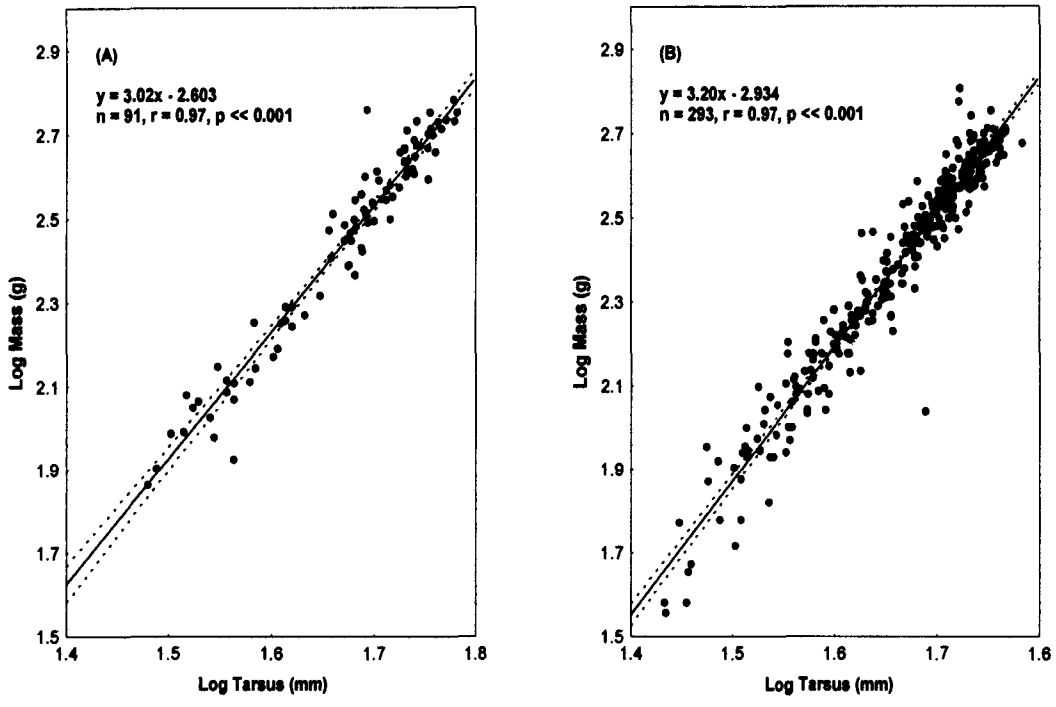

Fig. 4.6. Body condition (log mass/log tarsus) of oystercatcher chicks on Saldanha Bay islands (A) pre-*Mytilus* and (B) post-*Mytilus* invasion.

There was no difference in body condition between chicks from one- as opposed to two-chick broods in Unprotected Mainland Areas: neither the slope ($t_{(2),202}$ = 1.09, p >0.05) nor the elevation ($t_{(1),203}$ = 1.02, p>0.05) of regressions differed between single chicks and siblings. The same pattern was evident for chicks from Protected Mainland Areas (slopes: $t_{(2),42}$ = 1.76, p>0.05; elevations: $t_{(1),43}$ = 1.62, p>0.05). However, the body condition of chicks from one- as opposed to two-chick broods, was different for chicks reared on islands. (slopes: $t_{(2),560}$ = 3.43, p<0.05).

There was no difference in the body condition of first- *vs* second-born chicks, for chicks reared on islands (slopes: $t_{(2),102} = 1.15$, $p>0.05$; elevations: $t_{(1),123} = 1.62$, $p>0.05$) or on the mainland (slope: $t_{(2),40} = 1.36$, $p>0.05$; elevation: ($t_{(1),41} = 1.35$, $p>0.05$).

Surprisingly, and contrary to prediction, chicks on Saldanha Bay islands were in better condition before the *Mytilus* invasion than subsequently (Fig. 4. 6).

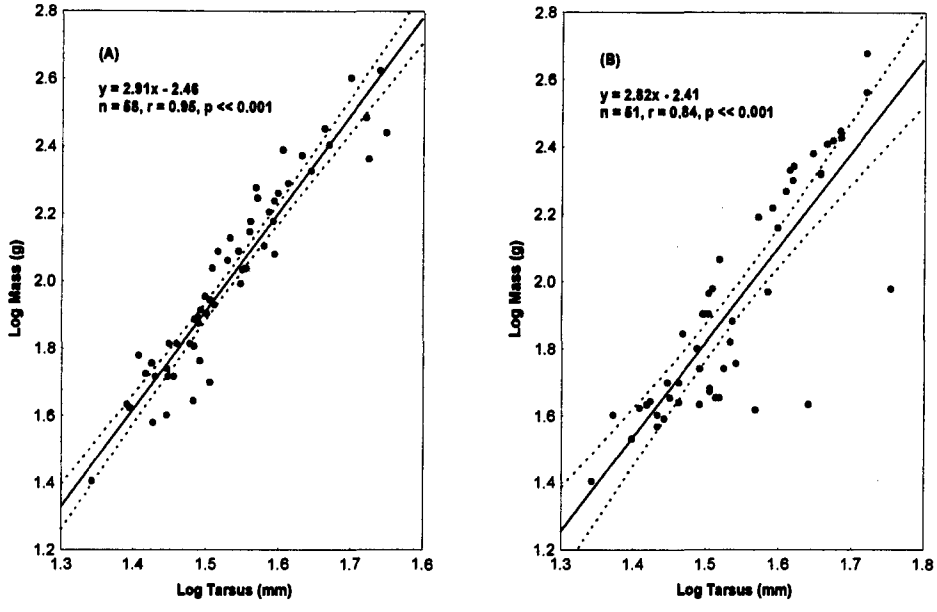

Fig. 4.7. Comparison of body conditions of chicks that (A) survived and (B) died before fledging.

Although the regression coefficients for pre- and post-*Mytilus* chicks did not differ ($t_{(2),292} = 1.89$, $p>0.05$), the elevation of the regression line for pre-*Mytilus* chicks was significantly higher ($t_{(1),293} = 3.08$, $p<0.05$), indicating that differences in body condition were evident from a very early age.

There was also a difference in body condition between chicks that survived and those that died before fledging (slope: $t_{(2),103} = 3.96$, $p<0.001$; Fig. 4.7). However, if the three chicks in very poor condition are excluded from the latter data set (6% of the data), this significance falls away (slope: $t_{(2),100} = 1.02$, $p>0.1$; elevation: $t_{(1),101} = 1.23$, $p>0.05$).

In summary, (but excluding the impact of body condition on fledging probability) three significant differences were obtained by comparing chick body condition indices under different scenarios. Body condition differed between a) chicks at unprotected mainland sites and on islands, b) two-chick broods and one-chick broods on islands, and c) chicks reared before and after the *Mytilus* invasion. Conclusions (a) and (b) above are based on differences in regression slopes, whereas conclusion (c) is based on a (statistically testable) difference in elevations. If slopes are different, elevations cannot be statistically compared (Zar 1996). However, in the context of this study a statistical difference in slopes is viewed as a scenario which can only be interpreted as a difference in chick body condition: however, no conclusion can be drawn as to whether one group is in better or worse body condition.

Despite the shortcomings of these statistical procedures, inspection of regressions for body condition of chicks on islands and at unprotected mainland sites (a) above) indicated that the regression line for island chicks generally lay well above that for mainland chicks, with the two regression lines intersecting near the origin. This strongly suggests that over most of the growth period island chicks are in better body condition than chicks in unprotected mainland areas. A similar inspection indicated no equivalent, obvious divergence in the regression lines for body condition of chicks from one- as opposed to two-chick broods on islands, although for the oldest chicks, chicks from one-chick broods did appear to be in better condition (i.e. have higher mass : tarsus ratios) than chicks from two chick-broods.

DISCUSSION

Given the unusual suite of constraints on foraging oystercatchers, both extrinsic (e.g. tidal limitations) and intrinsic (e.g. single-prey loading and full dependence of chicks on adults for food until well after fledging), it would be surprising if chick starvation never occurred. The index of body condition used here suggests that chicks that die before they fledge are, in a few instances, in very poor condition, and that this is likely to be the direct or indirect cause of mortality. However, data also suggest that overall, starvation is unlikely to be a major cause of chick mortality for the African Black Oystercatchers. Only three of the 51 chicks that died before they fledged were in obviously poor condition (Fig. 4.7). In general, visible evidence of poor body condition in oystercatcher chicks appears to be rare: >1500 oystercatcher chicks have

been ringed since 1997 and very few of these showed obvious signs of poor condition, even in the case of siblings (pers. obs.).

That human-induced chick mortality due to starvation is likely to be a rare event is further supported by model simulations. Even in areas of relatively low intertidal productivity (e.g. De Hoop N.R. and Goukamma N.R.), *ca* 30% of available foraging time would have to be lost on a continual basis before growth of a one-chick brood is significantly impacted, as defined by that chick entering a period of exponential mass deficit.

The model simulates disturbance in terms of a reduction in available foraging time. Human use of South African beaches is higher on weekends than in the week (Van Herwenden *et al.* 1989, Van Herwenden & Griffiths 1991, Prochazka & Kruger 2001) and higher in summer (when oystercatchers are breeding) than winter (Van Herwenden *et al.* 1989, Prochazka & Kruger 2001). However, no study has investigated whether there is any link between beach attendance and stage of the tidal cycle. It is clear that certain kinds of human activity are associated with low tide periods (e.g. bait collecting), but there is no *a priori* reason to assume that overall human activity (and associated disturbance) should be positively linked with low tide periods (when oystercatchers are foraging). Thus, to effect a 30% reduction in available foraging time is likely to require a much greater overall disturbance time (much of which will occur during the high-tide period, when birds are unable to forage). The model also does not explicitly address whether low-tide cycles fall during daylight hours or not. No systematic studies have been carried out to compare human activity on the South African coastline at day and by night, yet human disturbance is certainly very much lower at night irrespective of season or time of the week. To have a significant impact on chick growth, available foraging time would have to be reduced by an average of approximately 30% both day and night, even in regions of low intertidal productivity. This further supports the conclusion that, under most circumstances, disturbance to parental foraging time is unlikely to elevate chick mortality as a result of starvation.

The model is limited to cases where adults rear a single chick. However, based on comparisons of sibling body condition, and of one- *vs* two-chick broods, there is little evidence to suggest that starvation is ever a significant cause of chick mortality at the level of a local population. It is possible that the index of body condition used here was not sensitive enough to discriminate between real differences in condition.

Although tarsal length is a relatively conservative growth parameter (Hockey 1984a), studies of Eurasian Oystercatchers have shown quite marked variation in this parameter for slow-growing chicks as opposed to fast-growing chicks (Kirsten & Brenninkmeijer 1995). Studies of American Black Oystercatchers *H. bachmani* (Groves 1984) and Chatham Island Oystercatchers *H. chathamensis* (Schmechel 2001) have shown that two-chick broods do grow significantly more slowly than one-chick broods. In this study, however, there were insufficient data on chicks of known age to assess the degree of individual variation in tarsal growth rate.

Investigation of individual, simulated growth patterns for oystercatcher chicks for various disturbance regimes allowed identification of the point at which differences in mass (between a chick following the 'ideal' growth curve and chicks reared under simulated disturbance regimes) became exponential (i.e. reached the threshold), coinciding with the point at which negative growth was induced. Furthermore, simulated disturbances showed that it was very difficult to induce large mass differences (between 'ideal' and 'disturbed' chicks) without driving chicks into a state of negative energy balance. Studies of Eurasian Oystercatchers, where the growth of free-living chicks was tracked through time, indicate that death always occurred after a period of negative energy balance, rather than simply after a period of slow growth (Kersten & Brenninkmeijer 1995). Taken together, this suggests that in the rare cases where disturbance to foraging adult African Black Oystercatchers does lead to chick starvation, it is likely to occur when chicks are driven into a period of negative growth.

Although simulations allowed for identification of thresholds for chicks reared in different regions, thresholds were much more severe for continual disturbance regimes as opposed to weekend disturbance regimes (Fig. 4.4). Consequently, in the case of weekend disturbance regimes, relatively more foraging time (in excess of the threshold values) would have to be lost to induce a 50% mass deficit at the end of the chick growth period (Table 4.2). The reason for these differences is that in the case of weekend disturbance regimes, chicks were able to recover from periods of negative growth (during the period between weekends - e.g. Fig. 4.2b). In the case of a continual disturbance regime, once chicks were driven into a state of negative energy balance they were not able to recover – in these cases, any further reduction in parental foraging time simply increased the rate of negative chick growth.

Using a measure of 50% mass deficit is somewhat arbitrary. However, it probably represents close to the minimum chick mass required (relative to a healthy chick of equivalent age growing maximally), to survive the pre-fledging period. Even a localised study on African Black Oystercatchers (with small sample sizes) has shown that chicks of between 35 and 40 days old may have a mass deficit of 40% (compared to the fastest growing chicks of the same age) and still fledge successfully (Tjørve 2006). For Eurasian Oystercatchers this difference may even be slightly greater than 50% (Kersten & Brenninkmeijer 1995).

Most chick mortality in African Black Oystercatchers occurs in the first two weeks after hatching (Ch. 3). It can be concluded from this that human-induced chick starvation is not an important contributing factor to overall mortality, because energy requirements of large chicks, and hence foraging demands placed on adults, are much greater than those of the smaller chicks (which are the ones experiencing the highest mortality). Nevertheless, while far more parental foraging time has to be lost before chick growth is impacted for smaller chicks as opposed to larger chicks, if *Fb(t)* is compromised, any further reduction in parental foraging time is far more likely to drive a younger chick into a state of negative energy balance than an equivalent reduction in *Fb(t)* for an older chick. The reason for this difference is that smaller chicks have much less of an energetic 'buffer' between total energy requirements and *RMR* requirements (as modelled here).

Little is known about the difference between minimum energy requirements and total energy requirements in growing chicks in general. However a detailed study of changes in energy partitioning in free-living Arctic Tern *Sterna paradisaea* chicks (Klaassen *et al.* 1989) indicated as much as an eight-fold difference between the ratio of total energy requirements to basal energy requirements for a chick of 5 days old compared to one of 20 days old. In this study, comparison of calculated *RMR* using body-mass scaling, and total energetic requirements (as calculated for a captive chicks and adding 10% as the increase associated with free-living - see also Appendix 4.1) indicated a four- to five-fold difference, according to the error associated with *RMR* scaling. Thus even a once-off, but intense disturbance could lead to starvation and possibly death of small oystercatcher chicks, because such events have the potential to drive small chicks into a state of negative energy balance. Similar short, but intense events will also lead to negative growth in larger chicks, but larger chicks are more likely to recover from such a setback: supplementation of food to a Eurasian

Oystercatcher chick of approximately 40 days-old effected the chick's recovery from more than a week of negative growth (Kersten & Brenninkmeijer 1995). The same study demonstrated that the period over which a chick could endure negative growth increased significantly with chick mass.

By contrast, frequent, but small-scale disturbances to adults are unlikely to lead to chick death through starvation, because they are unlikely to induce negative growth in large chicks and unlikely even to impact on growth in smaller chicks (even in the case of two-chick broods - Leseberg *et al.* 2000).

There are three very important assumptions of the model: a) oystercatchers forage maximally and prey intake rates do not vary seasonally; b) after a disturbance event and an associated impact on chick growth, adults do not attempt to supply more food (through increasing their foraging time) than they would for a chick of the same age that had not experienced reduced or negative growth; and c) even if previously starved chicks were provided with an abundance of food, they cannot grow at a faster rate than an 'ideal' chick of equivalent age (e.g. Fig 4.2b). Thus, in this model, parental foraging time is not a dynamic variable, but is simply a function of chick age. Regarding the first assumption, when foraging times of adult Eurasian Oystercatchers were experimentally reduced (by varying tidal exposure times), the birds responded by increasing prey capture rates (Swennen *et al.* 1989). There is some fairly inconclusive evidence that the same species can increase prey capture rates when foraging time is lost to human disturbance (FitzPatrick and Bouchez 1998), although another study could not replicate this finding (Urfi *et al.* 1996). The second assumption reflects a lack of understanding, for the study species, as to how (or indeed if) adults respond to reduced or negative growth of their chicks. Unlike most other shorebirds, the pre-fledging provisioning of oystercatchers is entirely under parental control (Hockey 1996). In Eurasian Oystercatchers, there is much variation in the weight of chicks that fledge successfully, with most chicks growing below the maximum rate. Further, chicks with slow growth take much longer to fledge and experience reduced growth early in their life, long before energy requirements peak (Kersten & Brenninkmeijer 1995). It was concluded that much of the variation in growth rates and fledging mass may reflect a parental strategy, in the face of limited food, to adjust the future peak energy demands of their chicks to the maximum amount of food the parents are able to supply (Kersten & Brenninkmeijer 1995). Regarding assumption c) in the model, it is clear from a study of Eurasian

Oystercatchers that experimental food supplementation to a starved chick of approximately 40 days old (that had previously experienced negative growth) predictably allowed it to grow at a faster rate than non-starved chicks of equivalent age (because the growth rate of healthy chicks of equivalent age is already slowing considerably by this stage). It is not clear for African Black Oystercatcher chicks how much difference there may be in the maximal growth rate achievable by a chick that has been starved and the growth rate of a healthy chick of equivalent age. However, it is likely that there is some difference. This may explain why the difference in the impact of reduced foraging time on chick growth (expressed as a 50% mass deficit at the end of the growth period) for a weekend disturbance regime as opposed to a continual disturbance regime was not as great as might have been expected (see Table 4.2).

There is a link between decreasing intertidal productivity and decreasing adult oystercatcher foraging performance (Leseberg *et al.* (2000). It is possible that the invasion of the mainland coast by *Mytilus* may improve foraging performance and hence influence the predictions of the model presented in this study. At the Saldanha Bay islands the invasion by *Mytilus* in the 1980s was reflected in a concomitant increase in the proportion of *Mytilus* in the diet of oystercatchers and an increase in their breeding success (at least up until the early 1990s - Hockey & Van Erkom Schurink 1992). Counter-intuitively, however, this study demonstrated significantly worse body condition of chicks (several years) after the *Mytilus* invasion than previously: it is possible that this is a density-dependent effect. Although populations increased rapidly in the 1980s and early 1990s, since 1995 numbers have remained stable (Ch. 2). The proportion of *Mytilus* in the diet has also stabilised and the reproductive output of breeding oystercatchers, (measured as the ratio of one-to two-chick broods), having increased up until 1995, decreased and then stabilised, further suggesting a density-dependent effect on reproductive success (Ch. 2). In many areas of the South African mainland, however, *Mytilus* has only invaded more recently (Robinson 2005) and it is predicted that at these sites, foraging performance may well increase in the coming years, with a concomitant increase in chick growth rates and in breeding success. An improvement in breeding success may occur because improved foraging performance may lead to an increase in the average clutch size of oystercatchers (and there is some evidence that the number of three-egg clutches has increased in response to improved foraging habitats, as a result of the *Mytilus* invasion

- Ch.3). However, faster chick growth rates, as a result of improved parental foraging performance, may also play an important role in improving breeding success by reducing the window of vulnerability to other sources of mortality, especially predation (Hockey 1996, Ch. 3).

This study considers only the possible impacts of reduced growth of oystercatcher chicks on their survival up to fledging. As yet, there are insufficient data (due to the long period between fledging and return to natal areas) to relate reduced growth and low fledging mass to post-fledging survival. Although body condition has been linked to differences in dispersal strategies of juvenile African Black Oystercatchers (Hockey *et al.* 2003), it is not clear whether these different dispersal patterns translate into different juvenile survival rates. Among Eurasian Oystercatchers there is no evidence that differences in growth rate or fledging mass has any effect on post-fledging survival (Kersten & Brenninkmeijer 1995). In this species, the most important factor influencing post-fledging survival is probably the weather conditions over the first winter, with harsh conditions sometimes leading to mass mortalities, even of adults (Hulscher 1989).

Although African Black Oystercatchers do not experience equivalent bad weather (although storms can reduce their access to the intertidal zone), Paralytic Shellfish Poisoning and avian cholera periodically impact high-density breeding populations on South Africa's west coast islands (Hockey and Cooper 1980). Because a large proportion of the non-breeding population gathers in dense concentrations at localised areas and for extended periods of time on the west coast of South Africa and Namibia (Hockey *et al.* 2003, Rao 2005), these same factors could theoretically play a major role in post-fledging survival of African Black Oystercatchers, although to date there is no evidence that this is the case.

In conclusion, model results, and measures of chick body condition and mortality from areas with varying levels of human disturbance, suggest that chick starvation as a form of human-induced mortality is unlikely to be a widespread phenomenon. This in turn supports the conclusion of Chapter 3, that most chick mortality is instantaneous in nature.

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APPENDIX 4.1.

Development of a model relating parental foraging time to chick growth

The key steps in the development of the chick energetics model used to assess the impact of reduced parental foraging time on chick growth for birds reared in different regions on the South African coast, are given below. The development of the model includes key equations and assumptions for each of the steps involved. (A reference list pertaining to the development of the model is given at the end of this section).

Initial model development

The basic model describes the rate of change of mass of an oystercatcher chick as a function of yield (defined as the change in mass of a chick per unit mass of food eaten) and the rate at which the parents supply food to the chick, in the following manner:

$$\frac{dM}{dt} = Y(t) * \frac{dS}{dt} \quad \text{.....Eq. 4.1,}$$

where $\frac{dM}{dt}$ is the rate of change of mass of a chick, $Y(t)$ is the yield at time t and $\frac{dS}{dt}$ is the supply rate of food to a chick. It is important to note that 'yield', which can be defined as the rate of change of chick mass ($\frac{dM}{dt}$) per unit of food eaten (intake rate - IR) incorporates both the energy required for maintenance as well as for growth. Hence, in the model, the yield function is only meaningful if the food supply to the chick is in excess of that needed to satisfy at least its resting metabolic rate (*RMR*) requirements. To deal with situations where food supply is inadequate to meet even *RMR* needs, the model was later modified to allow a chick to use its own body mass to satisfy *RMR* needs, with the result that it experiences negative growth. Initially however, only positive growth was considered, in order for the model to be calibrated.

Because the aim of the model was to investigate the impact of reduced feeding time on chick growth, it was necessary to express the supply rate of food to chicks in terms of available feeding time. This was done using the following equation:

$$\frac{dS}{dt} = 2 * K * (Fb(t) - Fnb) \quad \text{.....Eq. 4.2,}$$

where K is the intake rate of an adult bird, $Fb(t)$ is the foraging time of a breeding adult at time t and Fnb is the foraging time of a non-breeder. Because intake rates for growing chicks were only available for captive chicks, the higher energy demands of a free-living chick were accounted for by conservatively increasing intake rates by 10% (Leseberg *et al.* 2000). It was also assumed that locating, handling and feeding prey to a chick took adults on average 20% more time than that required to feed just themselves, for a given quantity of food. This is also considered a conservative estimate (Leseberg *et al.* 2000). The numerical value "2" in Eq. 4.2 represents an assumption that both parents are feeding the chick simultaneously. Substituting in Eq. 4.2, Eq. 4.1 becomes:

$$\frac{dM}{dt} = Y(t) * 2 * K * (Fb(t) - Fnb) \quad \text{.....Eq. 4.3.}$$

By solving the differential equation (Eq. 4.3), it is possible to calculate the mass of a chick at time t as follows:

$$M(t) = M(0) + \int Y(t) * 2 * K * (Fb(t) - Fnb) \quad \text{.....Eq. 4.4.}$$

Input data and model calibration

The model was calibrated as follows. Energy intake data and mass data from a single captive oystercatcher chick (Hockey 1984a) were used to construct an energy intake curve, $IR(t)$ and growth curve $M(t)$. From these data the rate of growth, $\frac{dM}{dt}$ and hence $Y(t)$ could be estimated. Using empirical data on a) the average foraging time of a non-breeding adult bird (Fnb) at Marcus Island (Leseberg *et al.* 2000), b) the average available foraging time for an adult bird on Marcus Island (Hockey 1984b, Leseberg *et al.* 2000), and c) the surplus feeding time available to an adult provisioning a chick of 35-40 days old (Leseberg *et al.* 2000) it was possible to estimate a constant adult intake rate K and to generate a curve $Fb(t)$, which tracks the increase in foraging time required by an adult bird to satisfy its own energy demands

as well as those of a growing chick. Data from Marcus Island were used as a benchmark representing a situation approaching a best-case scenario. Out of all sites for which regional data on foraging times exist, adult oystercatchers at Marcus Island have to spend the least time foraging to satisfy their own energetic requirements (Leseberg *et al.* 2000), presumably because the population is below carrying capacity and the site is food rich (Ch. 2). The parameter K and the $Fb(t)$ curve were estimated

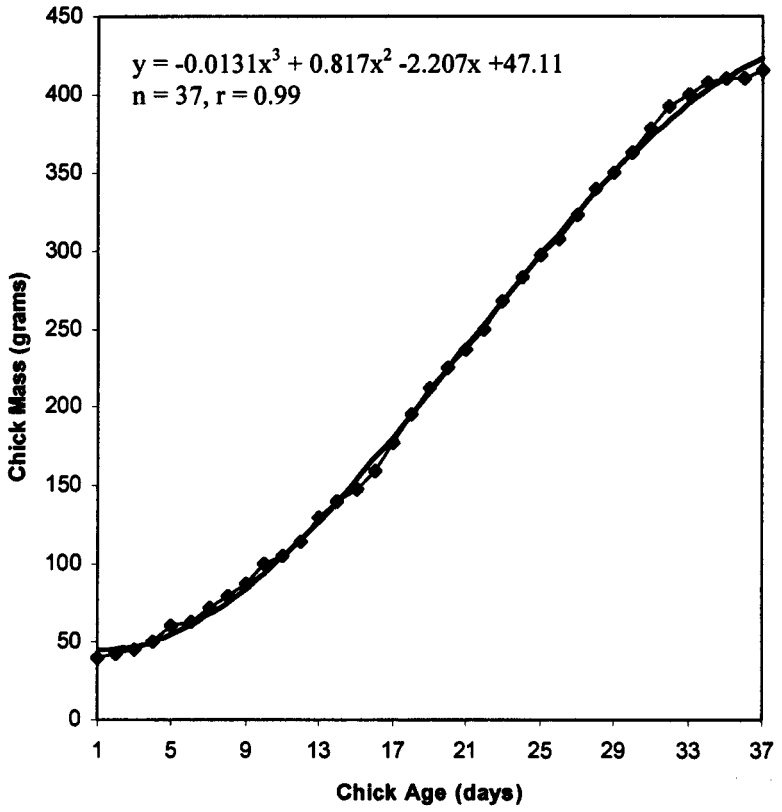

Fig. 4.8. Fitted curve for empirical growth data from a captive oystercatcher chick.

by running the model (Eq. 4.4) with different values of K to generate a growth curve which follows the empirically derived curve $M(t)$, while simultaneously generating a curve $Fb(t)$ which arrives at the same empirical estimate (c) above. Hence, in the context of the model and its calibration, the curve $Fb(t)$ represents the increase in parental foraging time with increasing chick age, under the most favourable circumstances. It was this parameter that was of most interest in the study, because it

is the one that needed to be manipulated in the model to investigate how disturbance to foraging parental birds (reducing foraging time) might impact on chick growth. The first step, therefore, was empirical derivation of $\frac{dM}{dt}$, *IR(t)* and *Y(t)* and then using the model to derive *Fb(t)* and *K*.

Estimation of $\frac{dM}{dt}$, *IR(t) and Y(t).* Growth data for an oystercatcher chick were taken from daily mass measurements of a single captive chick up to 37 days old (Hockey 1984a). The reason why these growth data were used is explained in the derivation of *Y(t)*. The growth data were smoothed and a function fitted to the growth curve. The growth curve is described by the following polynomial equation (see also Fig. 4.8):

$$M(t) = -0.013 * t^3 + 0.82 * t^2 - 2.21 * t + 47.11 \qquad (n=37, r=0.99) \quad \text{Eq. 4.5.}$$

Differentiation of this function provides an instantaneous growth rate:

$$\frac{dM}{dt} = -0.039 * t^2 + 1.636 * t - 2.207 \quad \text{Eq. 4.6.}$$

For the African Black Oystercatcher, the only data that exist where measurements of mass and intake rate (IR) were taken simultaneously come from five captive chicks that were supplied with food *ad lib* (Hockey 1984a), where the amount of food consumed (measured in kJ) and the mass of captive chicks (measured in grams) was recorded on a daily basis. Of these, for only one chick were there consistent growth measurements over the most rapid period of growth, thus only the data from this one chick were ultimately selected to determine *Y(t)*. In order to determine *Y(t)*, raw *IR* values were smoothed and a function fitted to the data. The function is described by the following 3-parameter Gompertz model (see also Fig. 4.9):

$$y = 929.398 * \exp 9 - \exp(1.49 - 0.07 * x)) \quad \text{Eq. 4.7.}$$

In deciding which regression models to fit to the data, the approach of Ratkowski 1990) was followed, *viz*, in the first instance, to try to use a linear regression model

with the lowest number of parameters possible. In the case of the raw mass data, the polynomial regression equation used fitted the data extremely well. Although Ratkowski (1990) suggests that simple polynomials of the type $y = a + bX + cX^2 + ...$

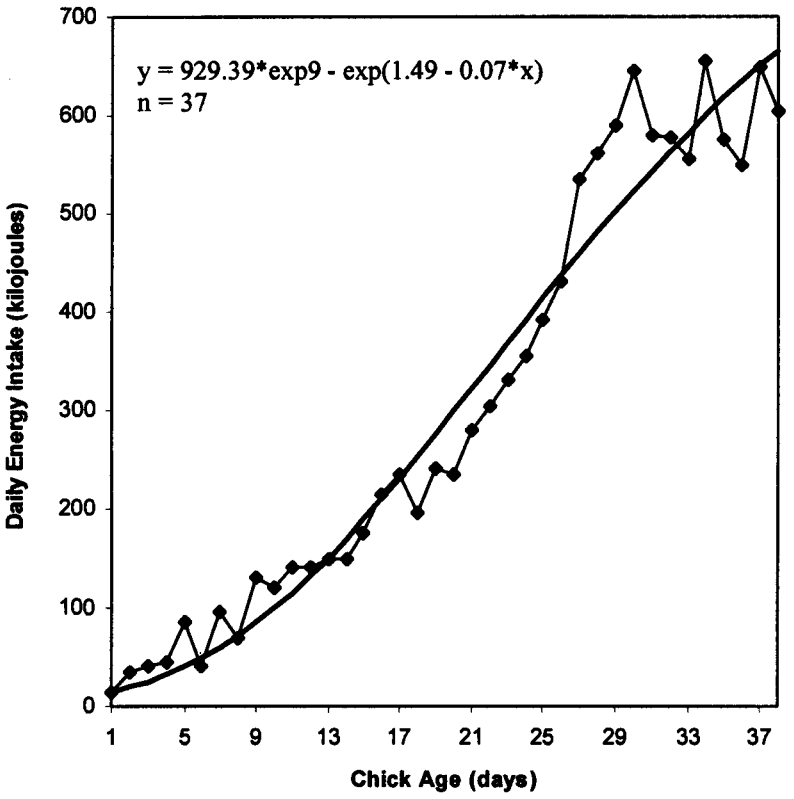

Fig 4.9. Fitted curve for empirical energy intake rate data from a captive oystercatcher chick.

should be avoided (because they seldom arise naturally in scientific work), the aim here was simply to smooth the data, so that it could be used in Eq. 4.4, which is an integral function.

Fitting an acceptable regression model to the energy intake (IR) data proved more difficult. No simple (low parameter) linear regression model fitted the data well. It was therefore decided to revert to a non-linear regression model. The 3-parameter Gompertz model (Ratkowski 1990) was chosen because it fitted the data reasonably well (low sum of residuals), with a fairly small number of parameters and hence exhibited close-to-linear behaviour (i.e. residuals were normally distributed). The r^2 statistic as a measure of 'goodness of fit' is meaningless for non-linear regression

models (Ratkowski 1990): in this case, the goodness of fit was deemed reasonable by inspection of the residuals.

Because *Y(t)* in the model is defined in mass units, it was necessary for IR values (which were energetic units ($kJ.day^{-1}$)), to be converted to mass units (grams wet $mass.day^{-1}$). To do this, food consumed was assumed to have a constant energetic value of 20 $kJ.g^{-1}$ dry mass. Although oystercatchers feed on a wide variety of intertidal organisms (Hockey & Underhill 1984), the most common prey species on rocky shores can be narrowed down to just three groups of intertidal organisms - mussels, limpets and polychaete worms - which have energetic values ranging between 18 and 22 $kJ.g^{-1}$ dry mass (Field *et al.* 1980, Branch & Newell 1978, Van Erkom Schurink & Griffiths 1991). To convert dry mass values to wet mass values, a conversion factor for intertidal limpets was used (Branch and Newell 1978): food items delivered to chicks were assumed to have an average water content of 85%.

Values generated from Eq. 4.6 and Eq. 4.7 were then used to calculate *Y(t)*, i.e.:

$$Y(t) = \frac{Eq.4.6}{Eq.4.7} \quad \text{.....Eq. 4.8.}$$

It is necessary to emphasise that the estimate of water content of food items delivered to chicks is of particular importance, because the relationship between water content of food and the energetic value per unit of wet food mass is not linear. For instance, if the energetic value of food is 20 $kJ.g^{-1}$ dry mass, and the water content is 85%, then the energy value per unit wet mass is 5 $kJ.g^{-1}$. However, if the water content increased to 90%, the energy value of the food per unit wet mass more than halves, to 2 $kJ.g^{-1}$. This point is reflected in Fig. 4.10, which illustrates *Y(t)* curves generated using a range of water content values for food items delivered to chicks.

Whether the average water content value used here is reasonable is open to question. It is likely that there may be some variation in water content between the most important oystercatcher prey species. However, most of the variation in water content of food items delivered to chicks is likely to arise through differences in the circumstances parental birds are subject to while feeding their chicks (i.e. time of day at which low tide occurs, time prey items are exposed to the air before being delivered to chicks etc.) and therefore cannot be easily accounted for in the model.

Estimation of Fb(t) and K. In order to run the model, differential equation integrator software Aquasim v2 was used (Reichert 1998). This program allows variables (*Y(t)* in this case) to be entered as a formula or as a listed variable (a list of discrete values). To calibrate the model, and later use the model for simulations, *Y(t)* was simply entered as a listed variable, rather than as a formula, because *Y(t)* itself was derived from fitted functions (see Eq. 4.8) and, as can be seen from Fig. 4.10, is

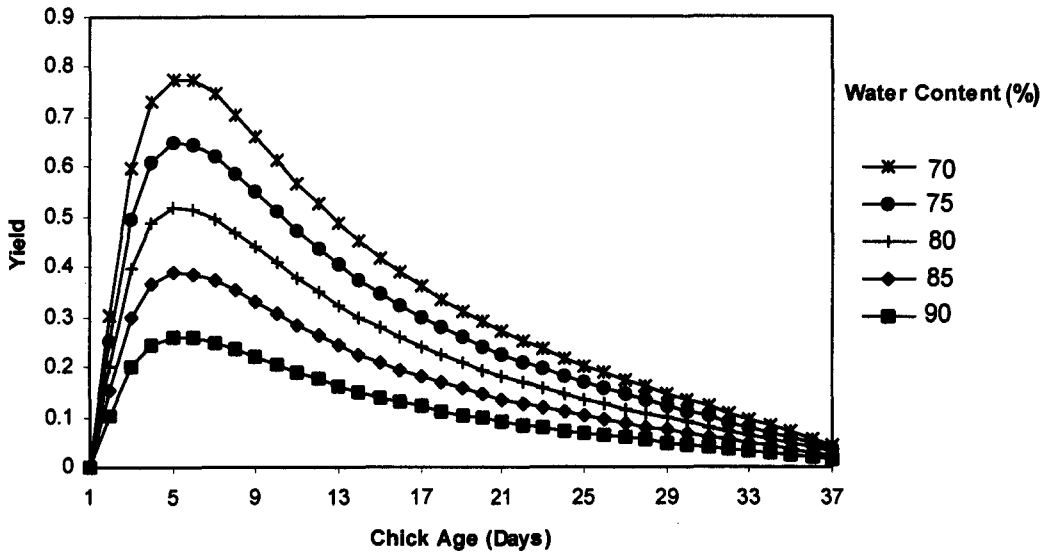

Fig. 4.10. Variation in yield curves according to variable water content of the food. Yield is expressed here as the unit change in chick mass per unit of food consumed and is a dimensionless parameter. Note that the maximum yield decreases almost by a factor of four with a 20% increase in the water content.

already a smoothed curve. To enter *Y(t)* as a formula into the programme would first require fitting a regression equation to the data - this would only be necessary if *Y(t)* were not a smooth curve, or if it was intended for *Y(t)* to be manipulated a number of times in the model (in which case it is useful to have an equation which can be adapted to various circumstances). In this model, the *Y(t)* curve is left unchanged. The latter statement implicitly assumes that the basic physiological processes occurring during chick growth – in particular the efficiency with which food is turned into biomass with time, and the way in which food energy is allocated to various activities over time, remain fundamentally the same for any growing chick, i.e. follow the same *Y(t)* curve for any chick. To initiate the programme, a starting mass (M_0) of 40 grams

(Hockey 1984a) and average daily foraging time for a non-breeder (*Fnb*) of 0.179 days (Hockey (1984b)), were used (all units for the model being expressed in terms of grams and days). The model assumed that foraging rates for parent birds were equal, irrespective of whether they were feeding during the day or night.

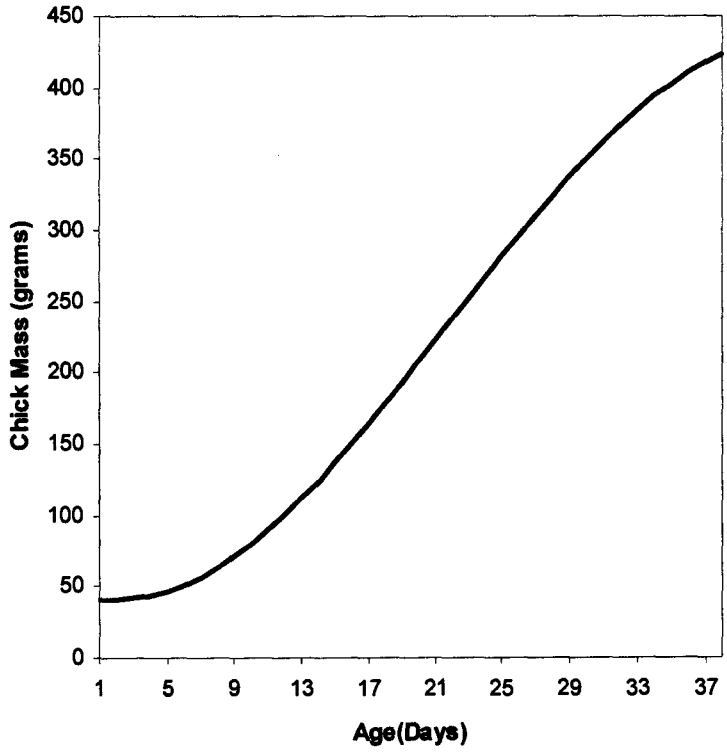

Fig. 4.11. Simulated growth curve for an oystercatcher chick, based on the energetics model.

Using Eq. 4.4 and Aquasim v2, the model was run for various values of *K* until the appropriate conditions were met - i.e. the empirically derived growth curve for an oystercatcher chick was adequately approximated and, simultaneously, that the *Fb(t)* curve generated resulted in the correct amount of surplus foraging time for a 35-40 day old chick (see *Calibration Approach*). An intake rate (*K*-value) of approximately 3 $kJ.min^{-1}$ (or expressing this rate in terms of grams and days – 1440 $g.day^{-1}$) adequately satisfied the above criteria – this suggests that the model is a reasonable approximation of the field situation. Independent field estimates of intake

rates of African Black Oystercatchers on rocky shores suggest intake rates vary between 2.3 and 3.2 $kJ.min^{-1}$, according to region and tidal regime (Leseberg 1998, Wilhelm 1999). The 'ideal' growth curve generated by the model is illustrated in Fig. 4.11.

The effect of a disturbance on chick growth was then examined by manipulating *Fb(t)* (the feeding time for a breeding bird) and comparing the resultant growth curves with the 'ideal' growth curve (refer to Methods (this chapter) for details).

Determination of RMR for a growing chick and modelling of negative growth

As it stands, the model cannot allow for negative growth (i.e. allow for a bird to use its own body reserves as an energy source). In the model, the growth rate only becomes zero if *Fb(t)* = *Fnb* (see Eq. 4.3). In reality, however, it is clear that there must be some point at which the energy supply to the chick is insufficient to support even resting metabolic needs and this will occur before *Fb(t)* = *Fnb*. The problem arises because the yield function does not explicitly address energy required for growth as separate from other energy costs. This does not matter, provided the energy supply to the chick is sufficient to at least support basal energetic requirements. If it does not, then the model no longer holds, because the chick must use its own body reserves to satisfy the energy deficit.

To overcome this problem, and to model negative growth, three additions were made to the model. Firstly, a criterion had to be established for determining the point at which the growth of a chick becomes negative. Secondly, a switch function had to be developed so that the growth of the chick became negative under the appropriate circumstances. Thirdly, the process of negative growth, or endogenous respiration, had to be modelled.

Establishing a criterion for negative growth using resting metabolic rate scaling.

There is no simple answer to establishing a criterion for the point at which the growth of a chick becomes negative. This is due to a lack of understanding as to exactly how a growing oystercatcher chick responds behaviourally and physiologically to food shortages.

Putting aside the question of negative growth, simply establishing the extent to which an oystercatcher chick's growth is slowed due to lack of food is a complex

problem in itself. There are a variety of possible options available to a growing chick facing a less-than-ideal food supply, in terms of how it responds to an energy deficit (i.e. an energy supply less than that required for 'ideal' growth). For example, it could keep growing at the same rate, but become much less active, or grow much more slowly while still maintaining the same level of activity, or make a compromise between these strategies.

In this model, the way the yield function is developed implicitly assumes that an energy deficit is spread between all activities (including growth) in ratios that are consistent with those incorporated in the yield function for an 'ideal' chick. In the case of positive growth therefore, a decrease in the food supply to a chick leads to a change in the growth rate, but the yield function remains the same and, in the model, is dependent only on the age of an 'ideal' chick.

To model negative growth, the resting metabolic rate (*RMR*) of a growing chick was used as the switching point between positive and negative growth.

To establish the *RMR* of a growing oystercatcher chick, a quadratic regression equation derived from an analysis by Weathers and Siegel (1995) was used. *RMR* here refers to measurements of metabolism made on chicks that were resting within their thermoneutral zones regardless of time of day, light levels or nutritional status. This must be distinguished from basal metabolism, since few of the studies used by Weathers and Siegel (1995) to establish the underlying scaling conformed to the criteria for basal metabolism *sensu stricto* (Williams and Prints 1986, Klaassen *et al.* 1989). The equation describes the relationship between *RMR* and body mass for a growing chick, using log-transformed data. As Weathers and Siegel (1995) point out, it is unusual to use a quadratic equation to describe log-transformed data (traditionally, linear equations have been used to describe these data and establish the underlying scaling). However, there is good reason to accept that the relationship between resting metabolic rate and mass, at least in the 27 species studied, is non-linear. In their study, Weathers and Siegel (1995) do establish two other methods to estimate chick *RMR* from body mass. However, these were discarded for two reasons. The two other methods discriminate between altricial and non-altricial species. Assuming that oystercatchers fall into the non-altricial group in their study (no oystercatcher species was used to develop the relationship between body mass and *RMR*) then, firstly, for non-altricial species, the scaling of *RMR* with body mass appears to be biphasic (i.e. there are two distinctly different linear relationships for

chicks at different ages), but the break point varies considerably: using a mean for predictive purposes may be very misleading. Secondly, not all non-altricial species in the study displayed a biphasic relationship between *RMR* and body mass.

Weathers and Siegel's (1995) quadratic equation relating *RMR* to body mass for a growing chick and based on an analysis of 27 species, is:

$$\log RMR = -1.4852 + 1.2684 \log M - 0.102(\log M)^2 \quad \text{.....Eq. 4.9,}$$

where *RMR* ($kJ.hr^{-1}$) is the resting metabolic rate of the chick and *M* is the mass (g). To apply the above scaling relationship to a growing oystercatcher chick, *RMR* was derived using the growth curve for an 'ideal' chick (Fig. 4.11).

Weathers and Siegel (1995) point out that estimating *RMR* using Eq. 4.9, should be on average within ± 20% of the actual value. Given this fairly large margin of error, it was decided to consider a 'best-case scenario' and decrease *RMR* requirements as predicted by 20%. Although Weathers and Siegel's (1995) method for determining *RMR* is ultimately based on mass, there are many other factors which affect measurements of metabolic rate. These include illumination levels (Pohl 1969), time of day (Aschoff and Pohl 1970) and also whether chicks have fasted prior to measurement (Weathers *et al.* 1983). Age, nutritional status and body composition are also known to affect metabolic rates in growing chicks (Daan *et al.* 1990). These factors are not considered in the determination of *RMR* for an oystercatcher chick. *RMR* in the model is dependent only on the mass of an 'ideal' chick at time *t* as determined from Eq. 4.9. Hence, it is important to note that a starved chick will experience the same *RMR* requirements as an 'ideal' chick of the same age. Weathers and Siegel (1995) clearly indicate that *RMR* values predicted from mass measurements alone are likely to be *higher* in fed than in fasted chicks. However, no attempt has been made here to adjust *RMR* values to account for this because there are no data with which to make a reasonable correction (one with narrow confidence intervals) to the current scaling relationship.

To switch between positive and negative growth, the model tracks the energy supply (ES ($kJ.day^{-1}$) derived from Eq. 4.8) to the chick through time along with the *RMR* requirements ($kJ.day^{-1}$) for a growing chick, as derived from Eq. 4.9. Provided that ES > *RMR*, the model follows the positive growth function. Any energy

deficiency experienced by the chick is apportioned in accordance with the yield function of an 'ideal' chick – i.e. *RMR* is not explicitly modelled. When the energy supply to the chick falls below *RMR* requirements, the model switches to the negative growth function, where *RMR* becomes an explicit component in determining mass loss. The function developed to describe mass loss is expressed mathematically as follows:

$$\frac{dM}{dt} = \left[2 * K * (Fb(t) - Fnb) - RMR(t)\right] * C \quad \text{.....Eq. 4.10,}$$

where $2 * K * (Fb(t) - Fnb)$ is the energy supply (ES) to the chick (unchanged from Eq. 4.2), and *RMR(t)* is the resting metabolic requirements at time *t*. The difference between *ES(t)* and *RMR(t)* in this function is negative by definition and describes the rate at which a deficit in *RMR* develops. In the framework of the model, which assumes that a chick must satisfy at least *RMR* requirements as determined by Eq. 4.9, this deficit has to be accounted for through endogenous respiration. The parameter *C* in Eq. 4.10, converts this energetic deficit rate into a rate of mass loss $\frac{dM}{dt}$. To calculate C, data from Odum *et al.* (1965) on heats of combustion for dry tissue from non-migratory birds were used as a surrogate for the energy released through endogenous respiration under aerobic conditions. The value used is approximately 26 $kJ.g^{-1}$ dry biomass. To complete the calculation, 70% water content for oystercatcher chick biomass was assumed, giving 1 gram of chick biomass an equivalent energetic value of 7.8 kJ under oxidation. The water content value used comes from a study of adult Eurasian Oystercatchers (Marcström & Mascher 1979).

Although the heats of combustion for different organic materials do vary, they depend almost entirely on the gross chemical composition (i.e. proportion of fats, proteins and carbohydrates) of the material in question (Morowitz 1968). For example, the same migratory bird species can have quite different heats of combustion due to widely varying fat contents at different times in the migratory season (Odum *et al.* 1965). Similarly, it is quite likely that a growing oystercatcher chick's gross chemical composition will change through time and this may significantly affect heats of combustion and hence estimates of energy released through endogenous respiration.

It is well known that growing chicks may vary considerably in gross body composition and the importance of developing fat reserves in growing chicks (particularly among seabirds) has been well studied (O'Connor 1977, Weathers *et al.* 1983, Klaassen *et al.* 1989, Taylor & Konarzewski 1989, Reid *et al.* 2000). Water content may also vary with age in growing chicks (O'Connor 1977, Klaassen *et al.* 1989, Taylor & Konarzewski 1989).

Despite the fairly extensive literature on changes in lipid levels and water content in growing chicks in general, there appears to be nothing in the literature dealing with these parameters for the Haematopodidae. Existing studies of changes in gross body composition in the Haematopodidae and shorebirds in general have tended to focus on seasonal changes in lipid levels and water content in migratory adult birds, rather than those occurring in growing chicks (Baker 1975, Marcström & Mascher 1979, Daan *et al.* 1990). Given this lack of information, and for the sake of simplicity, no attempt has been made in the model to account for any possible changes in gross body composition (e.g. percent lipid composition) or percentage water content with chick age.

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CHAPTER 5

ADULT SITE FIDELITY AND NATAL PHILOPATRY IN THE AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI*

INTRODUCTION

Several lines of evidence suggest that widespread local increases in African Black Oystercatcher *Haematopus moquini* numbers have occurred since the early 1980s, collectively resulting in a significant global population increase (Ch. 2). However, while the extrinsic factors of increased protection and enhanced food supply (Ch. 2) have undoubtedly increased the birds' breeding success (Ch. 3), philopatry, site tenacity and the age-at-first-breeding are all also important considerations in explaining population dynamics (Lack 1967, Burger & Gochfeld 1986, Hanski 2001). In particular, local population increases have to be considered in the context of possible permanent, small-scale movements of pre-breeding or nonbreeding oystercatchers with subsequent settlement as breeding adults, which may lead to rapid population increases at a local scale that cannot be accounted for by locally improved breeding success. Indeed, many local population increases of oystercatchers have been too rapid to be explained by improved breeding success alone (Ch. 2, Ch. 6). Thus, an understanding of the movement patterns of both juvenile birds and nonbreeding adults, as well as the possible causes of these movements is potentially of great importance in understanding and predicting local population changes. Movement patterns of young oystercatchers of three years old and less are now fairly well understood (Hockey *et al.* 2003, Rao 2005). However, virtually nothing is known of the biology of African Black Oystercatchers potentially able to breed, but which have not yet become established as breeders ('floaters'). Yet, in the context of the species' conservation, these are important in assessing the status of local populations. Age-at-first-breeding is known to be a very important determinant of population growth rates, particularly in long-lived animals that experience delayed maturity and produce few young at each breeding attempt (Heppel & Crowder 1998, Heppel *et al.* 2000, Saether and Bakke 2000). Likewise, permanent movement of juveniles or adults

away from natal sites to other areas may increase connectivity between local populations and improve the status of otherwise isolated populations (Root 1998, Saether *et al.* 2005). Some species within the Haematopodidae are known to display high levels of natal philopatry (Hockey 1996b), and adult African Black Oystercatchers display very high site tenacity (Hockey 1983a). However, little is known about the degree of natal philopatry in African Black Oystercatchers, although there is some evidence for a high return rate of juvenile birds to natal breeding grounds (Hockey 1983a,b). Long-term site-faithfulness is almost certainly widespread in the Haematopodidae, occurring both in the most migratory species, Eurasian Oystercatcher *H. ostralegus*, and the most sedentary species, African Black Oystercatcher. In the former species, site-faithfulness is high both on the nonbreeding (Ens & Cayford 1996) and the breeding grounds (Hulscher *et al.* 1996). Given such high site fidelity of adult birds, together with the formation of long-term pair bonds that are characteristic of most and possibly all oystercatcher species, the potential exists for high levels of natal philopatry (Hockey 1996b) and there is ample evidence that this is the case for Eurasian Oystercatchers (Ens *et al.* 1996).

However, even if natal philopatry and site fidelity are strong, very localised, permanent, habitat-related movements may be of importance in the context of local population dynamics and population regulation (Rodenhouse *et al.* 1997). Ultimately, understanding the reasons for these small-scale habitat shifts is likely to relate to the life-history decisions that potential breeders must make as to where and when to settle. Specifically, there are trade-offs involved, because high-quality habitats (areas with high food availability, good nesting habitat etc.) have higher densities of breeding birds than do low-quality habitats. Thus, potential breeders have to make a decision between waiting a longer time for good-quality habitat to become available where breeding success is likely to be high, compared to settling sooner in poorer quality habitat where breeding success is likely to be lower. Both theoretical (Ens *et al.* 1995) and empirical studies (Heg 1999, Heg *et al.* 2000, Bruinzeel & Pol 2004) of Eurasian Oystercatchers demonstrate that potential settlers must make a rather complex series of life-history decisions and that as a result of these decisions, queues of varying length form for different quality habitats. Furthermore, spending time in a queue and establishing local site dominance is an important factor in increasing the chances of establishing a territory in a particular habitat. An important rider to the so called 'queue hypothesis' is that individuals are not free to move between queues - in

leaving one queue to prospect for a territory elsewhere, an individual forfeits its position and local dominance in the queue it has left (Ens *et al.* 1995, Heg 1999, Heg *et al.* 2000, Bruinzeel & Pol 2004). For African Black Oystercatchers there is currently insufficient data to explore fully the behavioural biology of potential breeders. Nevertheless, there are now some data on individually identifiable birds of breeding age which have and have not established territories, to begin to assess whether, in this species, queues form for high-quality breeding habitats, specifically on islands, and to investigate the possibility of dominance hierarchies and local site dominance of potential breeders.

The latter phenomena are important in understanding local population dynamics and hence the conservation needs of the species. For example, the act of delaying breeding to increase an individual's lifetime reproductive success may lead to short-term depression of local population growth rates (Gordon 1997).

In the light of local population changes and the factors driving them, this study had three major aims: a) to assess whether and to what degree African Black Oystercatchers exhibit natal philopatry, (b) to ascertain the age at which they enter the breeding population, and (c) to identify the factors that might determine age-at-first-breeding.

METHODS

Population age structure

Between 1976 and 1997, more than 1500 oystercatchers were ringed (ringing taking place each year) during the breeding season, mostly on the Saldanha Bay islands. The majority of these birds were ringed as chicks with a metal ring only, although between 1976 and 1982, 236 adults also were ringed. In addition, over a period of three years between 1979 and 1981, 178 adults were individually colour-ringed with unique colour combinations (Hockey 1983a). These data provided the first opportunity to assess the age structure of oystercatcher populations on the Saldanha Bay islands (Malgas, Jutten and Marcus Islands (33°03'S, 17°58'E)) (Fig. 1.1), as well as make estimates of longevity and age-at-first-breeding for the species. During the 1998/1999 and 1999/2000 breeding seasons, pairs in which at least one partner was ringed were located and as many ringed birds from these pairs as possible were retrapped using walk-in traps on the nest. This method has been extensively used previously with no

recorded nest failures as a result of the trapping procedure (P.A.R. Hockey pers. comm.). In addition to retraps, a few breeding birds still retained colour rings from the 1979-1981 ringing seasons: the ages of these birds could be determined by direct observation. These data were combined with the data based on retraps of metal-ringed birds. Raw data were corrected for the number of birds ringed in a particular year and for yearly survival. Survival rates applied to year-cohorts were based on mean estimates of first-year survival (60%), average, yearly survival from one to four years of age (80%) and adult survival (96%) (D. Loewenthal & P.A.R. Hockey unpubl. data). Data were divided in to five-year age classes to give a frequency histogram of the proportion of birds theoretically surviving that were represented in the retrap/resighting sample from the Saldanha Bay islands.

Juvenile recruitment and natal philopatry

In addition to the ringing efforts between 1976 and 1997, from 1997 onwards an extensive colour-ringing programme was launched as part of a broader study to understand the movements of juvenile oystercatchers (Hockey *et al.* 2003, Rao 2005). From 1997 onwards all oystercatcher chicks located were colour ringed. Colour-ring combinations used codes for region and year-cohort, but from 1998 onwards, rings with individually engraved letters/numbers were used, making it possible for birds to be individually identified in the field. Colour rings (colours used in parentheses) were assigned to the Saldanha Bay islands (yellow) and Dassen Island (33°25'S, 18°05'E) (orange) and to five arbitrarily defined regions on the mainland coast of South Africa. These regions were (1) the west coast of South Africa, from Lambert's Bay (32°10'S, 18°20'E) to Cape Point (34°20'S, 18°30'E) (blue); (2) Cape Point to the Breede River (34°30'S, 20°55'E) on the south coast (red); (3) Breede River to Cape St. Francis (34°10'S, 24°55'E) (green); (4) Cape St. Francis to Cape Padrone (33°40'S, 26°35'E) (white); and (5) East of Cape Padrone (black/turquoise). Between 1997 and 2005, 1516 oystercatcher chicks were ringed in this way. Again, a large proportion of these (852) were ringed on west coast islands (532 on the Saldanha Bay islands and 320 on Dassen Island) where breeding densities and reproductive output are high. Between 1997 and 2005, ongoing yearly visits (2-3 times during the breeding season, between December and April) were made to the Saldanha Bay islands and during complete counts of oystercatchers, details of colour-ringed oystercatchers and status (single, paired, breeding) were recorded. Over the same period, local high-tide roosts on the

mainland (within a *ca* 50 km radius of the Saldanha Bay islands) were visited, with each roost being checked for colour- ringed birds 1-3 times, also over the breeding season. Roost sites checked in this way were: (1) Varkvlei (32°46'S, 18° 02'E); (2) Shell Bay (32°42'S, 17°58'E); (3) Hospital Point (32° 58'S, 17° 53'E); (4) Mauritz Bay (32°59'S, 17°53'E); and (5) Kleineiland Beach (33°08'S, 18°00'E). These observational data were used to compare the age structure of Saldanha island-reared birds on the Saldanha Bay islands, with the age structure of Saldanha island-reared birds at nearby mainland roosts during the breeding season. In a similar way to the analysis of the age structure of the breeding population on the Saldanha Bay islands using retrap data, the observational data were corrected for the number of birds ringed in each year-cohort and for survival.

Natal site fidelity of oystercatcher chicks reared on either Malgas or Jutten Islands were compared using three kinds of data: (1) observations of individually colour-ringed birds present during island counts made in the breeding season; (2) data based on birds ringed as chicks and retrapped as adults; (3) data based on birds ringed as chicks and recovered dead. In the case of observations and of recoveries, data were limited to birds >3yrs of age. This was done because a) the earliest age-at-first-breeding (for females) is known to be three (Hockey 1996a), and b) birds are quite frequently recovered dead, or observed on the islands, but these are often first-year birds which have not yet left the natal territory. The frequency of either observations, retraps or recoveries on the two islands were compared against the null hypothesis that birds are equally likely to visit and/or settle on either of the islands (independent of whether it is a natal island or not) and that the difference in frequencies of all the latter parameters between the two islands should therefore only be related to the area of each island. These analyses assume that the effort (either observational, recovery or retrap) is constant. This is likely to be a reasonable assumption, as both islands were typically visited the same number of times, within a few days of one another, on a yearly basis. Approximately the same proportion of the total number of ringed birds on both of the two islands was retrapped. Data on recoveries of dead birds and observations of individually identifiable birds were also gathered for chicks reared on the mainland and the same age criteria were applied. Numbers of either recoveries or observations of individually identifiable birds were compared in areas within 50 km of the natal site and more than 50 km from the natal site. The latter data, however

were not compared statistically as recovery and observation effort is likely to differ substantially around the coast, and it was not possible to control for this.

During the height of the 1999/2000 breeding season a survey of the coastline between the Berg River (32°40'S, 18°20'E) and Cape Point (a shoreline distance of 183 km) was undertaken to assess whether there had been any permanent movement of oystercatchers from west coast islands (particularly the Saldanha Bay islands, where birds have been regularly ringed over the past 28 years) to the adjacent mainland. At the time of the survey, very few individually colour-ringed birds of potential breeding age would have been available because of the long time-span between when adult birds were colour ringed (late 1970s/early 1980s) and when this survey was undertaken, and also because relatively few adult birds were originally colour ringed (very few individually colour-ringed birds from ringing efforts in the late 1970s/early 1980s were observed during the course of this study, thus the focus was on identifying metal-ringed birds. The number of metal ringed birds and their position on the coastline was noted. Breeding pairs with at least one partner possessing a metal ring were identified and an attempt was made to retrap these birds on the nest to determine their origins. The possibility that birds of potential breeding age reared on islands are also more site-faithful to roosts adjacent to natal islands (and possibly use these roosts as staging grounds from which to make forays onto natal islands to attempt to establish territories) was assessed by comparing the number of observations of colour-ringed oystercatchers greater than and less than or equal to three years old reared on Dassen Island at roosts adjacent to Dassen Island with birds in the same age classes reared on the Saldanha Bay islands. A similar comparison was made at roosts adjacent to the Saldanha Bay islands. The closest roosts to the Saldanha Bay islands were: (1) Varkvlei (32°46'S, 18° 02'E); (2) Shell Bay (32° 42'S, 17°58'E); (3) Grootpaternosterpunt (32°44'S, 17° 53'E); (4) Paternoster (32°46'S, 17°54'E); (5) Cape Columbine (32°50'S, 17°50'E); (6) Hospital Point (32° 58'S, 17° 53'E); (7) Mauritz Bay (32°59'S, 17°53'E); and (8) Kleineiland Beach (33° 08'S, 18°00'E). The closest roosts to Dassen Island were at Yzerfontein (33°21'S, 18°15'E) and Koeberg (33°48'S, 18°32'E). Oystercatchers up to three years old are unable to breed, and are highly mobile, exhibiting complex dispersal and migration patterns (Hockey *et al.* 2003, Rao 2005). It was thus hypothesised that there should be no difference in the frequency of observations of these age classes either of Saldanha Bay island birds or Dassen Island birds either at roosts near Saldanha Bay islands or

at roosts near Dassen Island. On the other hand, if birds more than three years old are using these roosts as staging areas to make forays onto natal islands, observation frequency of Dassen Island birds at roosts near Dassen Island was hypothesised to be greater than that for Saldanha Bay birds, and *vice versa* for observation frequencies at roosts near Saldanha Bay. Observation frequencies were compared against the null hypothesis that observation frequencies are related only to the numbers ringed on either Dassen Island or the Saldanha Bay islands. Survival rates for the two groups of birds in the analysis were assumed to be similar, as has been shown empirically for adults at Dassen Island and in Saldanha Bay (D. Loewenthal & P.A.R. Hockey unpubl. data). In addition to these analyses, a long-term data set from Goukamma Nature Reserve (see Ch. 2 for details) on the south coast of South Africa, which includes counts of breeding birds as well as nonbreeding birds over 14 years, was assessed. At this site, the breeding population increased rapidly between the early and mid 1990s and it was hypothesised that if local site dominance by nonbreeding adult is occurring (as suggested by Ens *et al.* (1995) and subsequently demonstrated for Eurasian Oystercatchers (Heg *et al.* 2000, Bruinzeel & Pol 2004)), then the increase in the breeding population should be concomitant with a decrease in the local nonbreeding population.

RESULTS

Population age-structure

Results from combined retrap and resighting samples (n=53) of breeding adults on the Saldanha Bay islands suggest that breeding oystercatchers, at least on these islands, are relatively old - frequently in excess of 25 years (Fig. 5.1).

The oldest known-age African Black Oystercatcher is a male colour- ringed as a breeding adult on Marcus Island in 1977 and (surprisingly) resighted far from its breeding territory, at Kommetjie on the Cape Peninsula (34°10'S, 18°20'E) in 2000 (Hockey *et al. in litt.*). Because males reach sexual maturity at four years of age (Hockey 1996a), this bird is calculated to be at least 28 years old (and is probably in excess of 30 years old because the age-at-first breeding of most individuals appears to be at least 5 years, and may often be greater on islands). Longevity estimates for the African Black Oystercatcher are almost certainly limited by historical ringing data, which go back only as far as 1976. Eurasian Oystercatchers are known to live in

excess of 40 years (Ens *et al.* 1996). Based on the assumption of a positive relationship between survivorship and body mass (Hockey 1996b), it is reasonable to assume that the longevity of African Black Oystercatchers should be at least as great and perhaps considerably greater, given that they are substantially larger, non-migratory and never experience sub-zero ambient temperatures (Hockey 1996b).

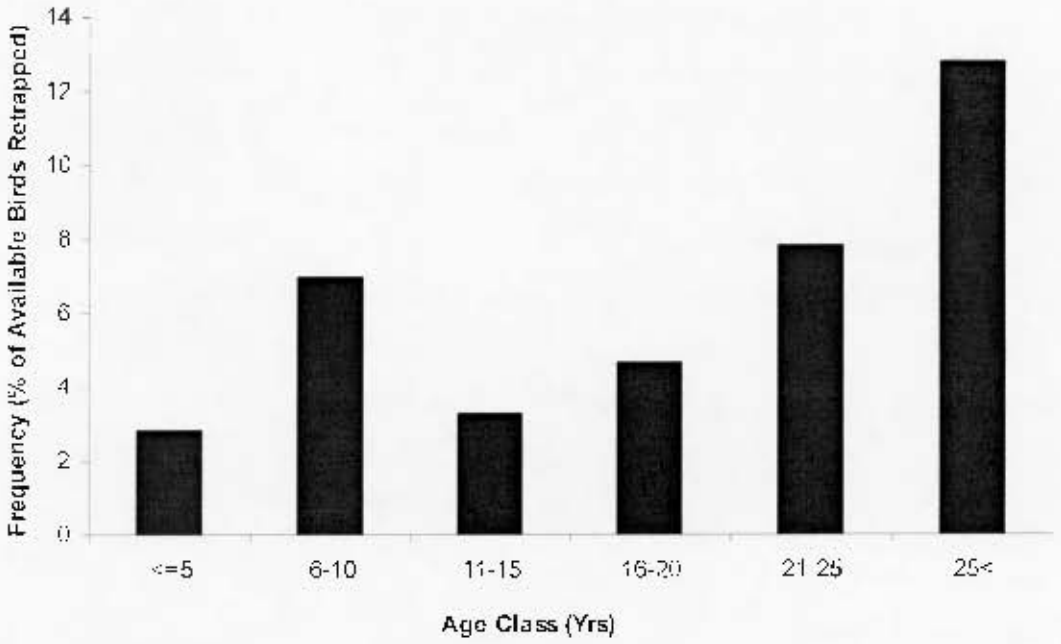

Fig. 5.1. Age structure of breeding adults on the Saldanha Bay islands. Data based on retraps of ringed adults, ringed either as chicks or as breeding adults, over 26 years, between 1976 and 2002. For birds ringed as adults, age estimates are based on age at sexual maturity for females (3) and males (4). Thus, estimates represent minimum ages. Data are corrected for the number ringed in each year-cohort and for adult survival.

Although the retrap sample indicates that some birds on islands do begin breeding at five years old and perhaps even younger, it also suggests that few birds begin breeding this early. Although observations of individually colour-ringed birds in this study were limited to seven years, the data suggest that there is an age hierarchy, in terms of an oystercatcher's progression towards becoming established as a breeding adult on the islands. While some non-breeding birds were present on islands when as young as two years old, there was a noticeable increase in the presence of non-breeding birds aged five to seven years. Similarly, the presence of paired birds increased progressively from five to seven years of age (Fig. 5.2). Birds at nearby mainland roosts, however, had a very different age structure. The highest

representation of oystercatchers was in the 2Y age class, with a progressive decrease in older age classes. No island-bred birds older than six years were present at local roosts.

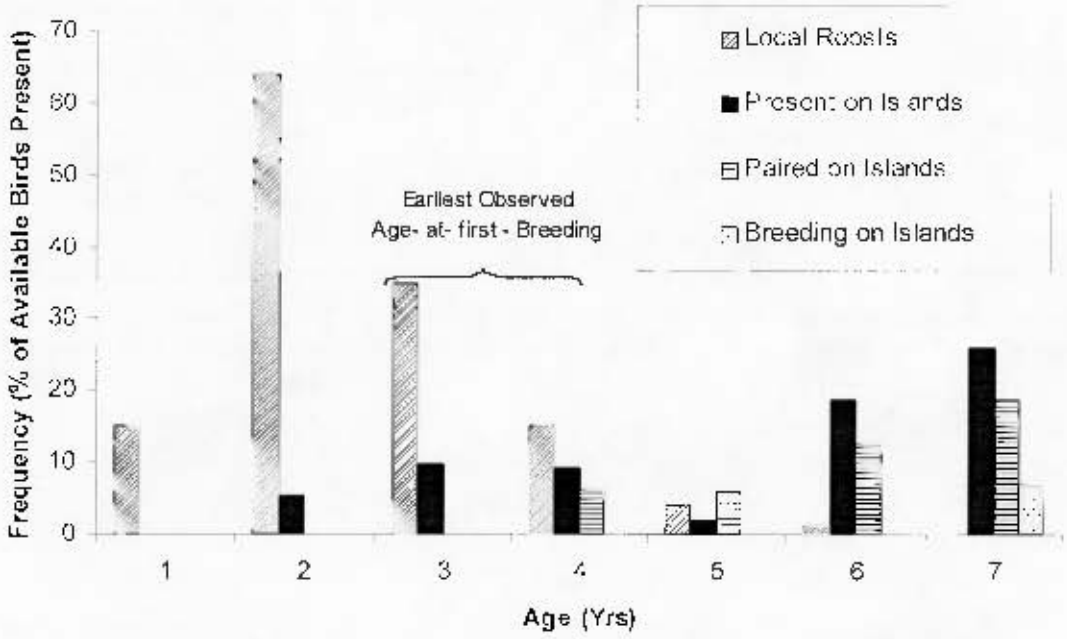

Fig 5.2. Age structure and status of oystercatchers reared on the Saldanha Bay islands, and resighted at local roosts (within a 50 km radius of Saldanha Bay) compared with those resighted on the Saldanha Bay islands. Data are based on seven years of resightings of individually colour-ringed birds and are corrected for the number ringed in each year-cohort as well as yearly survival (see text for details).

One-year-old birds were poorly represented at local roosts, but it is not clear why this should be. It could be argued that the lack of one-year-old birds at local roosts simply reflects their dispersal away from the vicinity of their natal sites in their first year. However, juvenile birds remain at dispersal endpoints for two to three years before returning to natal areas (Lesceberg 2001, Hockey *et al.* 2003, Rao 2005). Nonetheless, two- and three-year-old birds were relatively well represented at local roosts, making this an unlikely explanation. Although frequencies of birds of different ages on islands and at local roosts cannot be directly compared, due to differences in observation effort between the two localities, taken together the data suggest that,

from the age of two, non-breeding birds spend progressively more time on natal islands during the breeding season and less time at mainland roosts.

Natal philopatry

Island-reared birds exhibit extremely high levels of natal philopatry. In the case of Jutten and Malgas Islands, birds returned almost exclusively to their natal island. Related analyses of observational data, retrap data and recovery data (see Methods) were all highly significant (Table 5.1).

Table 5.1. Details of (a) individually colour-ringed nonbreeding oystercatchers >3 y old observed, (b) birds ringed as chicks and retrapped as breeding adults, and (c) oystercatchers >3 y old, ringed as chicks and recovered dead, on either Malgas or Jutten Islands. χ^2 analyses refer to comparisons for the two islands of (a) actual observations against the null hypothesis that observation frequencies are only related to island size, (b) actual number of retraps, against the null hypothesis that retrap frequencies are only related to the island size, and (c) number of recoveries against the null hypothesis that recovery rates are related only to the island size. All analyses incorporate Yates's correction for continuity.

Natal Island	No. of Observations			χ^2 Analysis	
	Jutten Island	Malgas Island	Total	χ^2_1	p-value
Jutten	20	4	24	7.74	<0.025
Malgas	1	27	28	44.32	<0.001

Natal Island	No. of Recoveries			χ^2 Analysis	
	Jutten Island	Malgas Island	Total	χ^2_1	p-value
Jutten	16	4	20	12.82	<0.001
Malgas	9	1	10	10.87	<0.001

Natal Island	No. of Retraps			χ^2 Analysis	
	Jutten Island	Malgas Island	Total	χ^2_1	p-value
Jutten	19	2	21	10.77	<0.005
Malgas	1	10	11	12.53	<0.001

On the mainland, recoveries and observations of individually identifiable colour-ringed birds also indicated high levels of natal site philopatry (Table 5.2), although this may in part be due to an autocorrelation between ringing and resighting or recovery effort (i.e. it is quite possible that there was most observer effort at

ringing sites). In addition, three birds, all five years of age, have been observed as paired (in all cases with an unringed partner and in all cases within 10 km of the natal territory). Two of these birds were resighted as breeding birds (with chicks) on the Keurbooms River on the south coast and one simply as paired, at Noordhoek (34°08'S, 18°22'E) on the western seaboard of the Cape Peninsula.

Table 5.2. Details of resightings and recoveries of individually identifiable oystercatchers >3 yrs old in relation to distance from natal site on the mainland coast of South Africa.

	Total No.	<50km	>50km
Recoveries of ringed birds	19	17	2
Observations of individually identifiable colour-ringed birds	26	22	4

Despite strong evidence for natal philopatry being the norm, there has been one conclusive instance of permanent movement away from a natal site. A bird ringed as a chick at De Hoop N.R. (34°29'S, 20°30'E) was resighted 150 km away as a five-year old breeding adult near Mossel Bay (34°13'S, 22°00'E) on the south coast of South Africa. [Note: Another bird ringed as a chick at De Hoop N.R. was resighted 246 km away five years later on the False Bay coast (34°05'S, 18°45'E). It appeared to be paired, but was only seen once and its status is unclear.]

The survey of the coastline between the Berg River and Cape Point at the height of the breeding season yielded only three metal-ringed birds. Correcting for the total number of birds metal-ringed in a particular year-cohort and for yearly survival (as was done for the more recent colour-ringing data) it is estimated that these three birds represent less than 1% of birds ringed on islands and of potential breeding age that were theoretically alive at the time of the survey. Of the three ringed birds located, two were on Yzerfontein beach (*ca* 33°20'S, 18°10'E), just to the south of Saldanha Bay and one at Paternoster (32°46'S, 17°53'E), 32 km north. All three birds were paired, but only two were proven to be breeding. It was only possible to determine the provenance of one of the two ringed breeders. It was ringed as bird of unknown age (but >1 year old) at a small roost at Langebaan in the West Coast National Park (33°09'S, 18°03'E) in 1992. Thus it could not be confirmed whether the latter bird was reared on the Saldanha Bay islands and there is therefore no conclusive

evidence of any permanent movement (either of adult breeding birds or birds reared as chicks on islands) away from the latter areas. These data further substantiate the conclusion that African Black Oystercatchers reared on islands exhibit extreme natal philopatry.

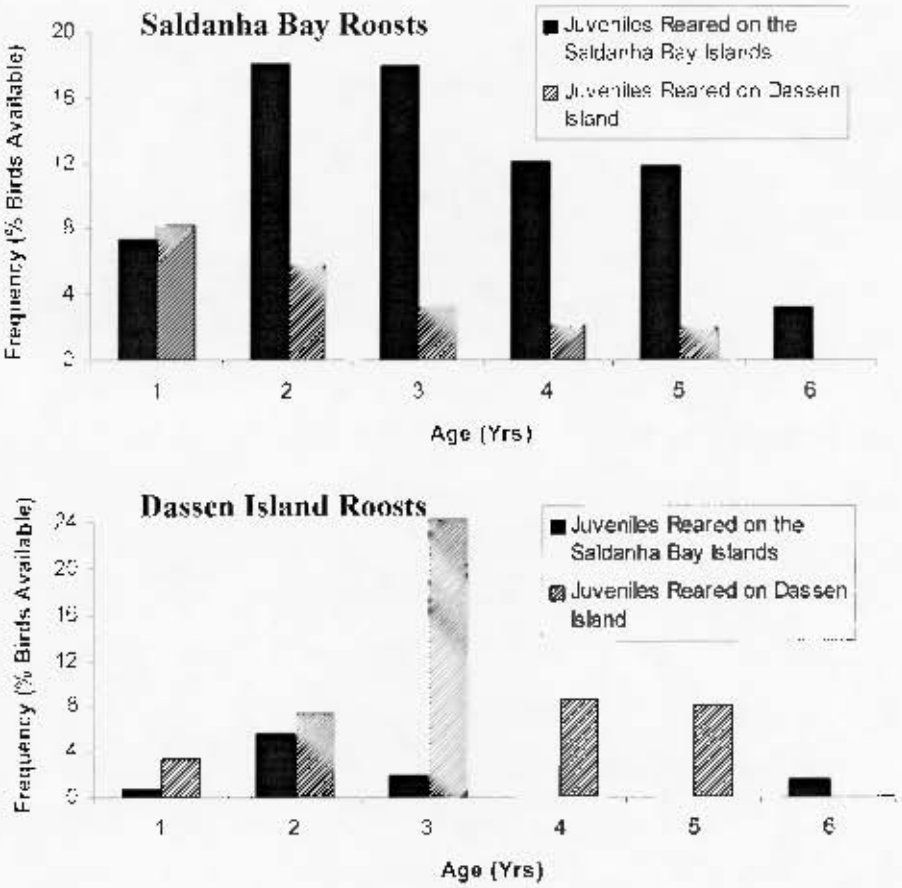

Fig 5.3. Age-structure of nonbreeding oystercatchers at roosts near Saldanha Bay islands and those near Dassen Island. Data are based on six years of observations of individually colour-ringed birds and corrected for yearly survival rates (see text) and the number ringed in each year-cohort.

Data from Dassen Island and the Saldanha Bay islands show that sexually mature oystercatchers are not only highly site faithful to natal areas, but also that they selectively utilise roosts adjacent to natal islands (Fig. 5.3). At roosts adjacent to Dassen Island, birds <3 y old, and reared on Dassen did not seem to show greater preference for these areas than did birds reared on the Saldanha Bay islands, in the same age class ($\chi^2_1 = 2.98$, $p>0.05$). However, birds >3 y and reared on Dassen were more frequent in roosts close to Dassen Island than were birds of the same ages from

Saldanha Bay (χ^2_1 = 53.98, p<<0.001). Similarly, at Saldanha Bay roosts, there was significantly higher representation of birds >3 yrs reared on the Saldanha Bay islands, compared with birds of the same age class reared on Dassen Island (χ^2_1 = 30.49, p<<0.001). However, birds <3yrs old and reared on the Saldanha Bay islands were also relatively more abundant at Saldanha Bay roosts than were birds reared on Dassen Island (χ^2_1 = 9.10, 0.001<p<0.005).

These data suggest that the majority of sexually mature, non-breeding oystercatchers reared on islands use mainland roost sites as staging grounds to make forays to natal islands. Multiple resighting data of individually identifiable colour-ringed birds from the Saldanha Bay islands in the latter category indicate that they shuttle between mainland roosts and natal islands and that this activity can continue over a number of years (Table 5.3).

Table 5.3. Details of multiple resightings of individually colour-ringed nonbreeding oystercatchers >3 y of age ringed on the Saldanha Bay islands. I = observed on natal island, R = observed at local roost (roost within 50 km of the natal island), E = elsewhere (at roost sites >50 km from the islands, or on islands other than natal islands). Time between first and last resighting varied between 1 and 4 years.

Two Resightings		Three Resightings		Four Resightings	
Resighting Pattern	**No. of Individuals**	**Resighting Pattern**	**No. of Individuals**	**Resighting Pattern**	**No. of Individuals**
I→R→I	17	I→R→I→R	6	I→I→R→I→R	3
I→I→I	4	I→I→R→I	4	I→R→I→R→I	2
I→R→R	3	I→I→I→I	1		
I→E→R	3	I→R→R→R	2		
I→R→E	3				

Observational frequencies were low, with islands only being visited 2-3 times a year and all roosts only 3-5 times year. It is therefore almost certain that birds make much more frequent trips between roosts and natal islands than these data indicate, and that individuals recorded only on islands from year to year also shuttle between the mainland and natal islands.

It cannot be conclusively proven that none of the birds that were resighted multiple times were breeders, although none was ever observed paired up or breeding between the first and the last observations, either at natal islands or on the mainland.

One individual which was resighted four times alternately at local roosts and on its natal island, between 2001 and 2005 was never observed with a partner.

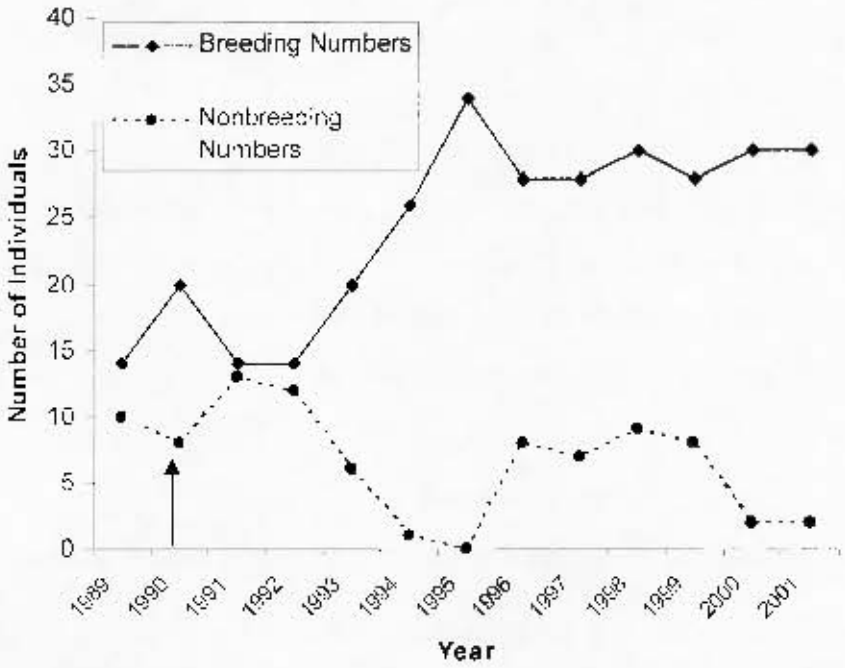

Fig. 5.4. Counts of breeding and nonbreeding oystercatchers during the breeding season at Goukamma Nature Reserve between 1989 and 2001. The arrow indicates the year in which protection status of the reserve improved significantly (see Ch. 7 for details).

At Goukamma Nature Reserve, concomitant with a rapid increase in the breeding population, the entire nonbreeding population disappeared. Furthermore, the increase in the breeding population was almost perfectly matched by the decrease in the nonbreeding population (Fig. 5.4). It was also evident that after the mid 1990s, when the breeding population stabilised, that the nonbreeding population increased, suggesting that nonbreeders which were present previously (but had not settled as territorial adults) had established some degree of local site dominance adjacent to the breeding areas.

DISCUSSION

High levels of adult site-faithfulness appear to be widespread amongst the Haematopodidae and this, together with the formation of long-term pair bonds

(typical of most, if not all oystercatcher species), means that natal philopatry is likely to be a ubiquitous phenomenon within the family (Hockey 1996a). This study of African Black Oystercatchers supports this conclusion, with the rider that spatial scale has to be factored in as an important parameter when drawing any conclusions with regard to levels of adult site fidelity and natal philopatry. Natal philopatry appears to be high on the mainland (at a scale of tens of kilometres), but this does not discount smaller-scale habitat shifts. Although resightings of individually identifiable colour-ringed birds breeding on the mainland indicated that these birds were breeding close to their natal territories, there are currently only three such records in total, two of which were of birds breeding within 10 km of where they were reared, but the third was of an individual breeding well outside the natal area (>50 km). Levels of both adult site fidelity (Hockey 1983a, this study) and natal philopatry (this study) appear to be extremely high for island oystercatchers, but these islands represent optimal habitats (with a rich food supply, largely free of predators and lacking human disturbance) where high site fidelity and high natal philopatry are likely to be favoured most of the time. The degree of site fidelity in sub-optimal habitats may be far more fluid.

One study of American Black Oystercatchers *H. bachmani* showed that not all adult breeding birds were site faithful and that site fidelity was based on the previous year's fledging success. Adults that successfully reared young to fledging were much more likely to retain the same territories in the following year than were those that were unsuccessful (Hazlitt & Butler 2001). It has also been demonstrated for Eurasian Oystercatchers that better quality habitats are more strongly defended than poorer quality ones, and that consequently some individuals wait years to obtain a good quality habitat whereas others fill poor quality ones quickly, but at the cost of reduced reproductive success (Ens *et al.* 1992). It is likely that a similar situation has arisen in the case of island-reared African Black Oystercatchers. In this study, birds as old as seven years (3-4 years after sexual maturity) were recorded still moving between natal islands and mainland roosts, even though breeding territories are widely available on nearby Marcus Island where the population has halved over the past 25 years (and presumably on the mainland as well, where densities are much lower than on islands). Ultimately, in the context of life-history theory, Ens *et al.* (1995) suggest that an individual's decision on when (at what age) to settle cannot be separated from its decision on where (which quality habitat) to settle. Thus, there is a trade-off between

waiting longer (with a higher risk of dying before breeding for the first time) for a high-quality territory (and concomitantly high reproductive success) and starting to breed sooner in a poorer quality habitat (with lower reproductive success). In the same study, it was suggested that in the case of higher quality habitats, the most likely path to obtaining a territory is establishing site dominance through spending time in a localised area. While the latter prediction was based on theoretical models of territory acquisition, it has since been demonstrated empirically for Eurasian Oystercatchers (Heg 1999, Heg *et al.* 2000, Bruinzeel & Pol 2004). A necessary outcome of this hypothesis is that hierarchies develop among queuing floaters in which those with the longest tenure have the greatest chance of achieving a breeding position. Although the data from this study are limited, it would appear that in the case of birds attempting to recruit into island breeding populations, a similar hierarchical pattern is established. From the age of sexual maturity, both the presence and status of African Black Oystercatchers (either paired or breeding) appears to increase with increasing age (Figs. 5.1 & 5.2).

African Black Oystercatchers of potential breeding age use sites on the mainland from which to make forays into high-quality breeding grounds (i.e. west coast islands). Potential breeders shuttle between mainland sites and high-quality breeding grounds and may spend years engaged in this activity. This pattern of behaviour has been widely reported in a range of species (Smith 1978, Newton 1998, Zack and Struchbury 1992) and three hypotheses have been invoked to explain the pattern. Visits are (1) attempts to aggressively remove territory owners (Arcese 1987), (2) reproductive strategies (floaters may gain parentage through laying eggs in the nest of a territorial pair or through extra-pair copulations) (Møller 1987), and (3) attempts to gather information. Information may relate to available breeding positions in the population (Struchbury & Robertson 1987), territory quality and reproductive success (the related behaviour is known as prospecting - Schjørring *et al.* 1999), or characteristics of an area and its associated territory owners (Stamps 1987).

Whatever the role of the latter behaviours are, sites near high-quality territories are clearly also of importance and may be contested by potential breeders. In this study, although data are limited, there was some evidence based on counts of both breeders and nonbreeders from the population at Goukamma Nature Reserve, that nonbreeding birds established natal site dominance and that this improved their chances of establishing a breeding territory in relatively high-quality habitat. Much

more detailed studies of Eurasian Oystercatchers have shown that potential breeders do exhibit territorial behaviour at communal gatherings (Ens *et al.* 1995, Heg *et al.* 2000) and there may also be a dominance hierarchy in these areas, based on site familiarity (Heg *et al.* 2000, Bruinzeel & Pol 2004). In the same species, site dominance near a breeding ground increases the probability of a bird obtaining a territory at that ground (Heg *et al.* 2000, Bruinzeel & Pol 2004). It was not possible in this study to demonstrate a relationship between local site dominance and the probability of obtaining a territory. However, it was notable that sexually mature birds reared on either Dassen Island or the Saldanha Bay Islands, were much better represented in roosts adjacent to their respective natal islands than in each other's local roosts, while for immature birds this difference was not nearly as pronounced. Thus, although the results of this study suggest a strong link between age and the probability of establishing a territory, it is not age *per se*, but rather time spent at a site that is likely to determine a bird's success in establishing a breeding territory.

The 'decision' of some individuals not to breed, even when capable of doing so, has consequences for population ecology (Gordon 1997) and identifying and understanding this behaviour may have important conservation implications. For example, the highly endangered Seychelles Magpie-Robin *Copsychus sechellarum* suffers from extreme habitat limitation with a carrying capacity of approximately 11 territories on the island of Fregate, and floaters already exist in a population of about 20 individuals (Komdeur 1996). Translocations of these 'surplus' birds to the neighbouring island of Aride, where they switched from floating to breeding, improved the reproductive output of the entire population, at least over the short term (Kokko & Sutherland 1998). A similar situation appears to have occurred with the reintroduction of the flightless Aldabra Rail *Dryolimnas [cuvieri] aldabranus* onto Picard Island, Aldabra where it had previously been driven to extinction, probably by terrestrial predators (which are no longer present - Wanless *et al.* 2002).

In the context of the African Black Oystercatcher, life-history decisions regarding whether to begin breeding sooner in poor-quality habitat or later in high-quality habitat are likely to have a strong influence on local population trends. Because some territories are clearly of exceptional quality and because oystercatchers are long lived, breeding may be delayed for many years as a strategy to optimise individual fitness. In cases of extreme differences in habitat quality (such as between Jutten and Malgas Islands and the adjacent mainland or Marcus Island), it is clear

from this study that birds may be prepared to wait a substantial time for a good-quality territory, even though lower quality territories are available. This accentuates differences in population densities between good and poor quality habitats that might otherwise only be due to trade-offs in breeding success between the positive benefits of better habitat quality and negative effects of conspecific crowding. The latter scenario is essentially described by the Ideal Free Distribution (Fretwell and Lucas 1972) which assumes that the reproductive success in a particular habitat is negatively impacted by competition with conspecifics. Thus, at equilibrium the average success of individuals is predicted to be the same across habitats, because high-quality habitats have higher densities of individuals (and thus experience density-dependent reproductive suppression) and *vice versa*. However, in African Black Oystercatchers, reproductive success is highest in high-quality habitats, despite high conspecific densities (Ch. 3) as has been amply demonstrated for Eurasian Oystercatchers (e.g. Ens 1992, Heg 1999). This is in keeping with an Ideal Despotic Distribution (Fretwell & Lucas 1972), whereby territorial individuals exclude nonterritorial individuals. However, the latter model requires consideration of lifetime fitness rather than immediate measures of fitness to explain why territorial individuals should be successful despots (Ens *et al.* 1995). The longevity of oystercatchers in general has hampered the possibility of measuring life-time reproductive success under different scenarios. However, several models have used game theory to explore, in the most basic sense, when the benefit to an individual from queuing for a high-quality territory balances the gain from occupying a poorer one immediately (the so called Evolutionary Stable Strategy) and to assess the population-level consequences (for both breeders and floaters) of these decisions (e.g. Ens. *et al.* 1995, Kokko & Sutherland 1998). In at least two very high-quality habitats (Jutten and Malgas Island) breeding populations appear to have reached an upper limit. Numbers on both the islands have remained essentially stable over the past 10 years, having increased dramatically prior to this (Ch. 2, Ch. 7). Several pairs are now occupying very poor habitats in the middle of these islands (pers. obs.). On Jutten Island, at least two pairs breeding on the island rear their chicks entirely from food brought from the mainland at least a kilometre away (feeding middens from these pairs consist almost entirely of *Donax serra*, which is a sandy shore bivalve, and hence comes from a habitat not present on the islands). Despite the very high oystercatcher densities on these islands (Malgas has arguably the highest density of any breeding oystercatchers in the world

with *ca* 60 pairs per kilometre of shoreline), this study suggests that there has been virtually no permanent movement of island-bred birds to the adjacent mainland. Assuming that breeding populations are now at carrying capacity, a population model, incorporating age-based recruitment into the breeding population, suggests that this situation is likely to persist under current conditions (Ch. 6).

Ultimately, predicting when oystercatcher populations in high-quality environments might (if ever) become sources for ailing populations, is likely to depend on the fitness consequences for individuals under different scenarios. Under current conditions, islands appear to be unlikely sources for supplementing ailing mainland populations, but the situation as regards permanent movement of birds between higher quality and poorer quality habitats on the mainland may be different.

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CHAPTER 6

POPULATION GROWTH RATES AND VIABILITY OF THE AFRICAN BLACK OYSTERCATCHER *HAEMATOPUS MOQUINI*

INTRODUCTION

Because of the ever-increasing pressure of humans on natural resources, understanding the factors which potentially render species vulnerable to extinction and the processes that eventually lead to extinction of wild populations have become major foci of biological research in recent decades. Processes leading to species extinction are often complex and interrelated, involving both environmental factors (such as quantity of suitable habitat and patterns of disturbance) as well as aspects of the species' life- history (such as reproductive output, longevity, dispersal behaviour etc.) (Soulé 1986). To disentangle this complex web of interactions, Gilpin & Soulé (1986) provided a useful framework for population vulnerability analysis (PVA) involving three fields of analysis: (1) population phenotype (including morphological, physiological and behavioural traits) (2) environment (including aspects of habitat quality and quantity and patterns of disturbance such as frequency, duration and severity) and (3) consequent population structure and fitness (which is dependent on the interactions between the first two components: aspects of population structure and fitness include the age structure, population growth rate and its variance). While the extinction of a species may be a very simple case of cause and effect (for example as a direct result of environmental destruction completely removing a species' habitat), the process of extinction is typically more subtle. In this context, Gilpin & Soulé (1986) identify two very important stochastic processes which may eventually lead to extinction: demographic stochasticity and environmental stochasticity. Demographic stochasticity is the chance variation in individual birth and death rates and is frequently the immediate precursor to extinction, with populations becoming vulnerable to this form of stochasticity when population numbers are low (Shaffer 1981). The routes by which populations are reduced to levels where they are vulnerable to demographic stochasticity are generally either through reduction in

habitat quantity or deterioration in environmental quality, mostly in turn as a result of environmental stochasticity. In the context of these forms of stochasticity and the vulnerability of populations to extinction, a species' life-history traits are extremely important (Koons 2005, Saether *et al.* 2005). For example, populations with potentially high growth rates (as a result of having high reproductive output and generally 'r-selected' characteristics) benefit from periods of good environmental quality (i.e. high food supply etc.) and can quickly increase in numbers, hence avoiding the risks associated with demographic stochasticity. Populations with typically 'K-selected' traits are less well adapted to the processes of environmental stochasticity and once reduced sufficiently in numbers, may remain for long periods of time in the zone where demographic stochasticity operates, significantly increasing the possibility of extinction (Seather *et al.* 1996, Seather *et al.* 2005). In the latter case, it has become of increasing importance in PVA to understand the relative importance of various vital rates (adult survival, fledging success, post-fledging survival etc.) and other life-history traits (age-at-first-breeding, longevity) to the population growth rate, because this can help guide management by concentrating efforts on those parameters that contribute most to the population growth rate (although some of these traits may not be manipulable through human intervention) (Heppel *et al.* 2000, Saether & Bakke 2000, Kauffmann *et al.* 2003, Jones *et al.* 2004). Other life-history traits such as high natal site fidelity may also increase a species vulnerability to reduction in habitat quantity and increased fragmentation (Root 1998, Saether *et al.* 2005). In the case of fragmented populations, the importance of connectivity of these populations in reducing the deleterious effects of demographic stochasticity and local environmental stochasticity has been widely demonstrated (Wilcox 1984, Soulé & Simberloff 1986).

Many of the above factors that place species potentially at risk of extinction are relevant to the conservation of African Black Oystercatchers *Haematopus moquini*. The African Black Oystercatcher is endemic to southern Africa, breeding on the coast and at offshore islands between Lüderitz, Namibia and southern Kwazulu-Natal, South Africa (Fig. 1.1). The current, total population size is fairly small and although the global population has increased over the last 20+ years (from *ca* 4 800 birds in the early 1980's to *ca* 6 670 birds in the early 2000s (Ch.2), numbers have decreased locally at 41 of 239 study sites along the coastline, mostly at sites where there has been a rapid increase in urban development (Ch. 2). Although all significant

island populations are well protected (Hockey 1983), the mainland coast of South Africa in particular continues to experience rapid development which is likely to fragment further the African Black Oystercatcher's already restricted linear coastal habitat. Adult *H. moquini* is highly site faithful (like most oystercatcher species worldwide) and young birds display very high natal site philopatry and adult site fidelity (Hockey 1996, Ch. 5). While the degree of natal site philopatry of local oystercatcher populations on the mainland appears to be high, but is not well known, there is very good evidence that the most productive populations - on the west coast islands of South Africa- are effectively isolated from mainland populations-there is currently no evidence of permanent movement of island-reared birds to the mainland (Ch. 5) limiting the options for source-sink dynamics which may potentially benefit fragmented mainland populations characterised by relatively low productivity. Furthermore, the growth rates of African Black Oystercatcher populations are limited by low reproductive output and high investment in young. Thus, even under very favourable conditions (high food productivity, low predation rates etc.) the population growth potential may be low, leading to long recovery times for populations reduced in number through stochastic processes associated with deterioration in environmental quality.

Possibly the most important form of environmental stochasticity that is known to have had severe, although localised impacts on African Black Oystercatcher populations, are periodic toxic algal blooms. Toxic algal blooms are a global phenomenon in coastal zones and negative impacts of these blooms on various forms of marine life have been recorded worldwide (Zhou *et al.* 1999, Irwin *et al.* 2003, Magaña *et al.* 2003, Sellner *et al.* 2003, Gayoso & Fulco 2004, Zhao *et al.* 2004). Globally (Landsberg 2002) and in South Africa (Kudela *et al.* 2005), the frequency and severity of toxic algal blooms appear to have increased in recent times and are likely to continue to do so, due directly to increased eutrophication of coastal waters from nutrient-rich effluent and indirectly due to an increase in favourable conditions for algal blooms, triggered by global warming (Siegfried *et al.* 1990, Peperzak 2003, Zhao *et al.* 2004). On a local scale, the risk of toxic algal blooms may also be on the increase due to particular species being introduced into local waters via ships' ballast (Hallegraeff & Bolch 1991, Doblin *et al.* 2004). African Black Oystercatchers are affected by toxic algal blooms through eating contaminated bivalves, which kill the birds via Paralytic Shellfish Poisoning (PSP) (Grindley & Nel 1968, Grindley 1969,

Hockey & Cooper 1980). PSP is caused by a neurotoxin synthesised by dinoflagellates. These dinoflagellates are accumulated in the flesh of filter-feeding bivalves, often making them highly toxic (Shilo 1967). Despite outbreaks of paralytic shellfish poisoning having been reported on numerous occasions in South Africa over the last century (e.g. Grindley & Nel 1966, Grindley & Nel 1968, Horstman *et al.* 1991, Probyn *et al.* 2001) there is only one case where PSP could be linked to a mass mortality of African Black Oystercatchers (Hockey & Cooper 1980). In this instance the impact, even at a population level was severe, with five high-density island populations being approximately halved during the outbreak (Hockey & Cooper 1980).

Although the latter case is the only instance where PSP was shown to have impacted oystercatchers at a population level, it is quite probable that PSP has had more frequent, but much less severe impacts on local oystercatcher populations and that these have gone undetected. In general, the negative impacts of toxic algal blooms are often underreported for various reasons (Sellner *et al.* 2003, Shumway *et al.* 2003). In the case of African Black Oystercatchers, corpses are rarely discovered – even after the massive PSP outbreak in 1978 only a few dead oystercatchers were discovered relative to the change in population numbers (Hockey & Cooper 1980). Even if corpses are found, the identification of PSP as the cause of death is not easy and relies on pathological analysis of freshly dead birds (Coulson *et al.* 1968).

High-density breeding populations of African Black Oystercatchers are almost certainly also impacted by periodic outbreaks of avian cholera - in 1999 populations on Malgas and Jutten Islands at Saldanha Bay, South Africa were reduced by approximately 30% and the number of corpses found during the breeding season were much higher than normal (pers. obs.). Again, it was impossible to make a diagnosis as no fresh corpses were found, but synchronous with this mass mortality, was a huge die-off of Cape Cormorants (*Phalacrocorax capensis*) and this is frequently indicative of an avian cholera outbreak (e.g. Donnelly 1966, Crawford *et al.*1980, La Cock 1986, Crawford *et al.* 1992). Whatever the reason for these mass mortalities, they certainly impact oystercatchers at the local population level, although the severity, frequency and locality are not readily predictable. Many of these mass mortalities probably go undetected because breeding populations may be quickly replaced by surplus pre-breeding birds accumulated in previous years. For example, the partial recovery of breeding numbers on the Saldanha Bay islands after the PSP

outbreak in 1978 was far too rapid to have been a result of a real increase in population size, because recruitment rate through reproduction is slow. (Age-at-first-breeding appears to be a dynamic variable dependent on breeding densities: even in low-density populations, the age at which birds recruit into the breeding population may be 5-6 years – Ch. 5).

Although oystercatcher populations on islands appear to be isolated from populations on the mainland, there is some evidence for permanent movement of oystercatchers between islands. In particular, natal philopatry may not always be island –specific and there are cases where birds reared on one island have established themselves as breeders on another island, although this seems to be rare (Ch.5). Despite evidence suggesting that there is little connectivity between island populations, the extent to, and conditions under which this occurs is unknown, yet it may be important in ameliorating the impacts of localised mass mortalities. Furthermore, under stochastic conditions – i.e. localised mass mortalities of breeding adults- birds reared elsewhere, including on the mainland coast of South Africa, may be encouraged to fill vacant breeding territories.

African Black Oystercatcher populations on the mainland coast of South Africa have been shown (both in this study-Ch. 3) and elsewhere (Jeffery & Scott 2005, Tjørve 2006)) to have extremely variable inter-annual breeding success in terms of average number of fledged young per pair per year. Thus they may be vulnerable to the effects of demographic stochasticity at low population numbers. At the same time, connectivity between mainland populations may be important in ameliorating these effects. Although island populations appear to be isolated from mainland populations, there is evidence for permanent movement of individuals between mainland populations. However, as with degree of connectivity between island populations, the degree of, and reasons for connectivity between mainland populations is not well known or understood.

The act of delayed breeding is known to have important conservation implications (Ch.5) and certainly for island-reared oystercatchers it is clear that they may wait many years to gain a high quality territory on an island (usually their natal island) (Ch. 5). For sexually mature island-reared oystercatchers, there is good evidence that an age-based recruitment pattern operates, with older birds preferentially entering the breeding population ahead of younger ones (Ch.5). It is likely that a similar age-based recruitment pattern is operating in the case of other

oystercatcher populations in lower quality habitats (and there is evidence of delayed breeding in the case of mainland populations-Ch.5), but the pattern is less pronounced, probably because sexually mature nonbreeding birds on the mainland don't have to or are not prepared to wait as long for a breeding territory to become available, compared with their island-reared counterparts (Ch. 5).

Given that the African Black Oystercatcher's conservation status is cause for concern, but that there are aspects of the species' biology which may benefit its conservation (such as its considerable longevity (Ch. 5) and some degree of connectivity between populations), the aims of this chapter are two-fold:

1. To develop, use and test a deterministic, age-structured model to measure the sensitivity of the intrinsic growth rate (λ) (particularly, the degree of change in λ) as a result of changing vital rates (e.g. fledgling success, adult survival) of oystercatcher populations under various protection scenarios.

2. To develop and use a series of stochastic models of oystercatcher population dynamics, incorporating (a) variability in breeding success; (b) simulated mass mortalities; and (c) different degrees of connectivity between populations to examine the impacts of these factors on oystercatcher population dynamics and viability.

The specific aims outlined above, highlight the general theme of the chapter, which is to use a series of population models, not in a predictive capacity, but rather to identify aspects of the bird's biology which are most important in influencing the viability of local populations.

METHODS

Definition of populations

Both for examination of intrinsic population growth rates and for stochastic model simulations, three types of oystercatcher populations were defined: (1) unprotected mainland populations (UMPs) (2) protected mainland populations (PMPs) and (3) island populations (IPs).

UMPs were defined as populations in those areas on the mainland falling outside of current marine protected areas (MPAs), nature reserves or national parks, and PMPs were defined as populations within such areas. IPs were defined as those populations on all off-shore islands and for analyses were grouped together as a single unit. The rationale for this definition is that there are significant differences in breeding success (success being defined as fledgings.pair^{-1}.year^{-1}) between these populations (Ch. 3). Despite large inter-annual variability, oystercatchers within protected areas on the mainland have higher breeding success than those outside protected areas, and island populations have 2-3 times higher fledging success than mainland populations (Ch. 3). Despite varying levels of human activity in protected areas, there are human-related factors operating in unprotected areas that impact negatively on oystercatcher breeding success and are not operating in protected areas. The extremely high breeding success of island populations is due to protection, but also lack of terrestrial predators and very high localised food availability (Ch.3). Calculations of intrinsic growth rates do not require any assumptions about initial population size. However, to initialise the stochastic models, population size had to be defined. Protected areas currently constitute 23% of the South African coastline (Lombard *et al.* 2004) and this, together with recent estimates of total mainland oystercatcher population size (Ch. 2), was used to establish the initial size of oystercatcher populations inside and outside protected areas. It is recognised that this is likely to bias the population size of oystercatchers inside protected areas because these are not uniformly distributed among bioregions - the entire Namaqua bioregion, which has small, but significant oystercatcher breeding populations currently has no protected areas, while the Delagoa bioregion (near the Mozambique border) with no breeding oystercatchers has over 20% protection (Ch. 2, Lombard *et al.* 2004).

Intrinsic population growth models

Intrinsic population growth rates (λ) were established for each of the defined populations based on a deterministic matrix projection model of population growth. Input data were breeding success (fledglings.pair^{-1}.per^{-1}) established from analysis of long-term nest monitoring data sets from the three defined populations (Ch. 3). Only single estimates (all to the nearest %) of adult breeding survival (mean= 96%), 1st year survival (fledging to 1 year old, mean = 60%) and subadult survival (average yearly survival from 1-4 years old, mean=80%) were available (Loewenthal &

Hockey unpubl. data): these were applied to all three defined populations. It is conceivable that 1st year survival, pre-breeding survival and adult survival are different for UMPs, PMPs and IPs, although there is no *a priori* reason to suggest that this is the case. First-year birds and subadults in particular are highly mobile and less subject to local phenomena impacting the breeding components of IPs, PMPs and UMPs, which could result in differential survival.

There is little data on longevity of African Black Oystercatchers. However, an adult male which was colour- ringed as a breeding adult on Marcus Island (33°02'S, 17°58'E) in 1976 was (surprisingly) resighted far from its breeding territory, at Kommetjie on the Cape Peninsula (34°10'S, 18°20'E) in 2000 (Hockey *et al. in litt.*). Because males reach sexual maturity at four years of age (Hockey 1996a), this bird is calculated to be at least 28 years old (and is probably in excess of 30 years old because the age-at-first breeding of most individuals appears to be at least 5 years, and may often be greater on islands-Ch. 5). Longevity was therefore set at 35 years of age. Male African Black Oystercatchers are known to have bred at 3 years old, and females at 4 years old (Hockey 1996). For all analyses (other than analyses examining the effect of varying age-at-first breeding, on λ) the minimum age-at-first-breeding was set at 4-years-old. However, there is now good evidence that age-at-first breeding is different for populations in areas of different habitat quality and, based on data from west coast island populations, may be a dynamic variable, largely dependent on breeding densities of populations in an area of given habitat quality (Ch. 5). Resightings of colour-ringed birds returning to natal sites and observed as breeders, suggests that age-at-first-breeding is 4-6 years for mainland populations, but could be as high as 10 years old for island populations (Ch. 5). Thus the effect of age-at-first breeding on λ was also investigated: age-at-first breeding for mainland populations was varied between 4 and 6 years of age and for island populations between 4 and 10 years of age, while keeping all other parameters constant at mean values. To test the effect of age-at-first-breeding on λ, pre-breeding survival rates were still only applied to birds up to 4 years of age (after which adult survival rate was applied). This was done (a) because there is only a reasonable estimate of average annual survival up to age 4 (Ch. 3), and (b) to avoid confusing the effects of lower survival rates on λ (i.e. more age classes with lower survival) with the impact of increasing age-at-first-breeding). It is probable that birds older than four years, but not breeding, have a lower survival than adult breeders (because they are still relatively mobile, often

flying relatively large distances, and do not have fixed feeding territories with a reliable food supply - Chapter 2) and, in terms of stochastic model application, a pre-breeding (> 1 year old) survival rate of 80% was applied, independent of age. In accordance with errors in estimates of vital rates, adult survival was varied between 94% and 98% (± 1 SD, to the nearest %), 1st year survival was varied between 45% and 75% (± 1SD, to the nearest %) for all areas and pre-breeding survival was varied between 72% and 88% (± 1 SD, to the nearest %). [Note: the relatively large degree of error in current survival estimates for 1st –year and pre-breeding birds, is due to survival estimates being based on resighting effort of colour ringed birds spread over a relatively large area (1st year and older pre-breeding birds are not sedentary and may move large distances before they settle as breeders-see Ch. 5)). There is thus a relatively high probability of not resighting live birds, leading to a relatively large degree of uncertainty in survival estimates for these age groups. However, both 1st year birds and older non-breeding birds congregate at relatively few traditional roost sites (Rao 2005, Ch. 5) allowing for resighting effort to be concentrated in these areas and giving currently usable survival estimates, despite the substantial overall length of coastline over which resightings have had to be made]. In each area, breeding success (fledglings.pair^{-1}. year^{-1}) was varied by 1 SD, giving the following values as input: UPMs (0.1-0.58); PMPs (0.23-0.61); IPs (0.78-1.04). λ-values for the various analyses were compared primarily to assess differences in the growth potential for the differently defined populations. However, the sensitivity of λ to the demographic parameters outlined above was also addressed.

Stochastic population models

Model development and structure

There are a number of existing pre-programmed software packages to examine population viability questions such as ALEX, RAMAS/space and VORTEX (Lindenmeyer *et al.* 1995). However, for reasons of understanding and also, because of some of the questions that wished to be addressed, it was decided to develop a new program. All models were written using the programming language TruBASIC Bronze Ed. (Kemeny & Kurtz 2000). It was also found to be easier to modify the existing model as developed here, to investigate density dependent effects on population dynamics (Ch. 7). The simplest form of the model took the following

structure. Two distinct populations were modelled – a breeding population and non-breeding population, with non-breeding birds not being allowed to enter the breeding population before they were at least four years old. Older non-breeding birds were given priority over younger pre-breeding birds in terms of recruitment into the adult population, thus age-at–first-breeding was modelled as a dynamic variable determined by the characteristics of the population in question (i.e. survival rates, longevity etc.). Again, the rationale for this is that there is good evidence from island populations that age- based recruitment is operating, and that older birds recruit into the breeding population before younger ones (Ch. 5). Breeding populations were fixed at an upper limit based on current census data – hence current breeding populations were assumed to be at carrying capacity (K).

In this set of simulations, possible density dependent effects, such as density- or site-dependent breeding success, were not implemented. Furthermore, no allowance was made for the fact that breeding populations might be influenced in a density-dependent manner (i.e. the total potential breeding population could not influence the number of breeders –cf. Ch. 7).

To initialise models mean vital rates were used and age-based recruitment was used as the default pattern of recruitment for all analyses. Thus, the initial conditions of the model provide a first assessment of the size and age structure of the non-breeding population. Also, because age-at-first-breeding was set by the demographics of the model, and because empirical data on age-at-first-breeding exist from a number of sites, it was possible to obtain some idea of the validity of the model. Because age-at-first-breeding is not a rigorous parameter to use for statistical model fitting compared to data on population age-structure (Moloney *at al.* 1994, McCarthy *et al.* 2000), and given that there is only very limited and localised data on population age-structure for *H. moquini* (Ch. 5), no attempt was made to fit the model to these data statistically.

A further reason why breeding and non-breeding populations were separated is that in the context of severe environmental stochasticity acting on localised breeding populations, it was of interest to examine how effectively the non-breeding population could buffer the effects of mass mortalities in the breeding population. Empirical data from islands on the west coast of South Africa (Hockey & Cooper 1980, D. Loewenthal pers. obs.) demonstrate that breeding populations may recover very quickly from mass mortalities - possibly due to an influx of non-breeding birds from a

"reservoir" of non-breeders accumulated over previous years, potentially masking mass mortalities.

Thus, estimating the size and characteristics of the non-breeding population is of key conservation importance, not least because the effects of mass mortalities in the breeding population are likely to be immediately apparent only in the non-breeding population. Even if mass mortalities are severe, it may be decades before this is readily detectable in the breeding population - by this stage, the pool of available non-breeders may be virtually depleted and the breeding population may quickly be reduced to near-extinction (see Fig. 6.1). To deal with simulations involving two separate types of breeding populations (unprotected and protected mainland breeding populations; impacted and non-impacted island populations), the same basic model was applied and initialised, but non-breeders from both breeding populations could potentially be used to replace adults from either of the two types of breeding populations (see also Fig. 6.2).

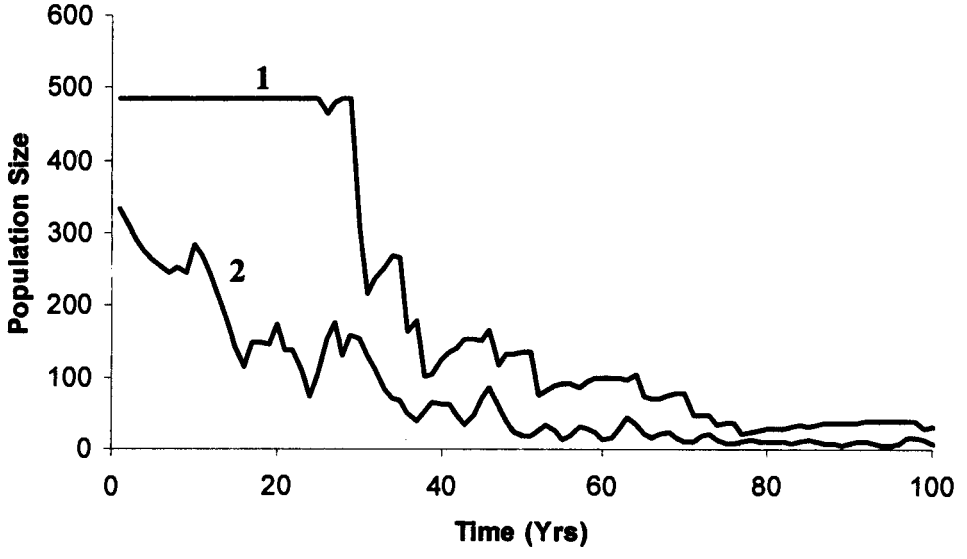


Fig. 6.1. An example of a single population simulation for a hypothetical African Black Oystercatcher population, where the adult breeding population experiences periodic mass mortalities (details below). In this particular example, the population decreases to the point of virtual extinction over 100 years. 1 = breeding population, 2 = non-breeding population. There is no detectable change in the breeding population for more than two decades despite an immediate decrease in the non-breeding population. Adult survival = 96% with a 1-in-10 year probability of a 40% reduction ; 1st-year survival from fledging = 60%; subadult survival = 80% and fledging success is variable (see text for details).

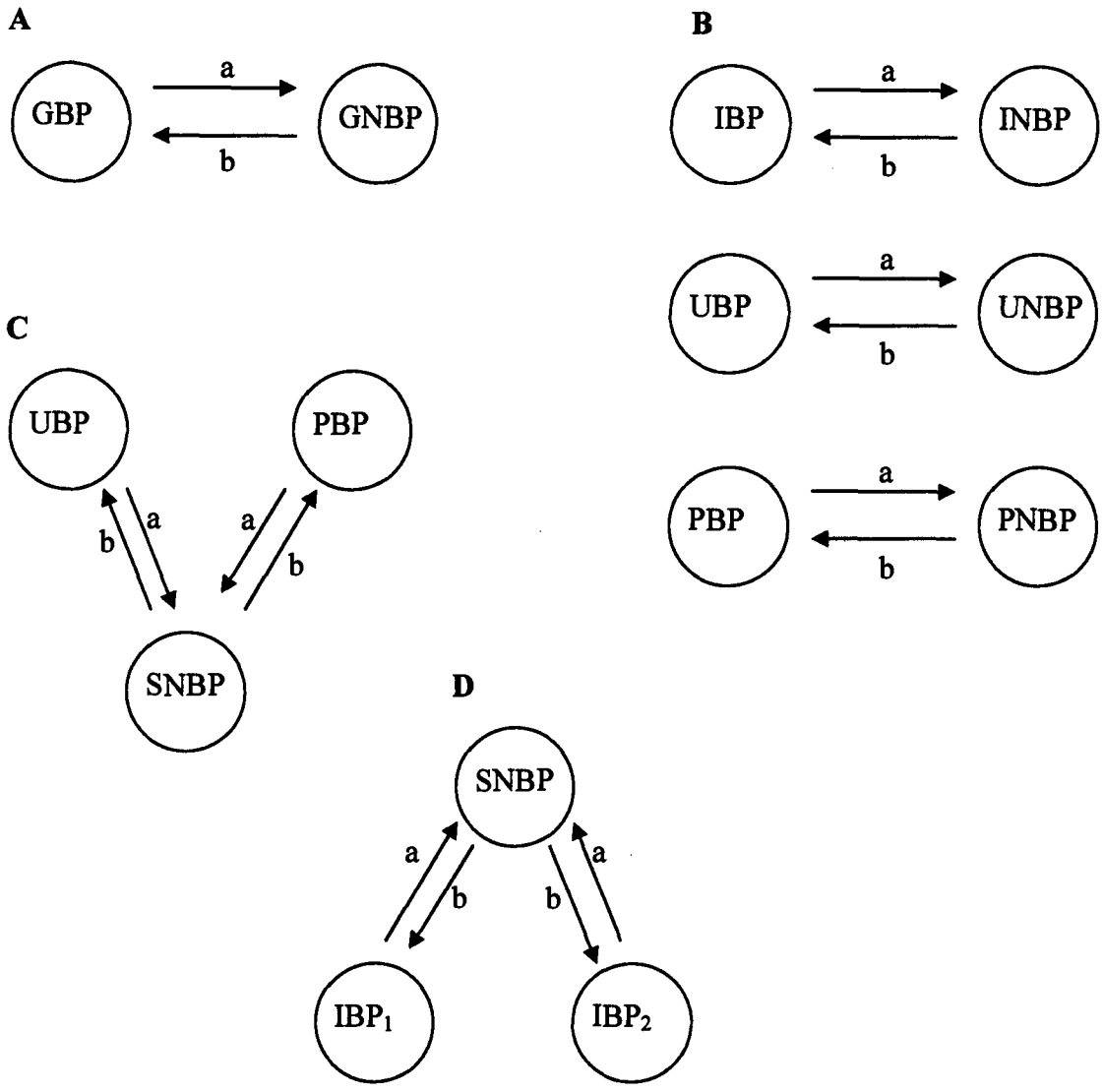


Fig. 6.2. Schematic diagram illustrating the four basic population models used in population viability analyses for the African Black Oystercatcher. Fig. 6.2A. The global breeding oystercatcher population (GBP) and non-breeding population (GNBP) are treated as single entities. Fig. 6.2B. The global breeding population is treated as three separate entities (island breeding population (IBP), protected mainland breeding population (PBP) and an unprotected mainland breeding population (UBP) each with their own non-breeding populations (i.e. island non-breeding population (IBNP), mainland protected non-breeding population (PNBP) and mainland unprotected non-breeding population (UNBP), respectively). Fig. 6.2C. PBP and UBP populations are treated as single entities, but with a shared non-breeding population (SNBP). Fig. 6.2D. Island breeding populations (IP) are treated as two separate entities with a shared non-breeding population. IBP_1 represents the fraction of IBP impacted by mass mortalities and IBP_2, the fraction not impacted. In all cases the upper limit to the breeding population is fixed. Birds enter the non-breeding population after fledging (arrows marked 'a'), while breeding adults that die are replaced by birds from the non-breeding population (arrows marked 'b'). For all analyses, models were constructed so that entry into the breeding population was age-based, with older birds having priority over younger ones. The minimum age-at-first breeding was set at 4yrs.

Population definitions

As with calculations of λ, three basic populations were identified and defined for the purposes of stochastic population simulations; UMPs, MPs and IPs. However, three further types of populations were defined for simulation purposes: (1) a global oystercatcher population (where the world population was treated as a single entity, although still with a separate breeding and non-breeding population); (2) an unprotected and protected mainland population with a shared non-breeding population and; (3) separate impacted (adult mass mortalities applied) and non- impacted island breeding populations with a shared non-breeding population (in this case, three treatments were applied in terms of the ratio of impacted (I) to non-impacted (NI) breeding populations (a) 25:75% (b) 50:50% (c) 75:25%. (Refer to Fig. 6.2 for details of all four basic model structures).

For each of these scenarios, breeding populations were recalculated (initial estimates of breeding population size for the three basic population types (IPs,PMPs and UMPs) were based on data from recent surveys - see input data) and initial conditions were set by running the model with mean survival rates, mean fledging success and incorporating age-based recruitment, to establish the non-breeding population and hence the total population size, in each case.

Input Data

Survival parameters: For all simulations, the same mean survival rates used for calculations of λ (*viz.* adult breeding survival - 96%, 1st-year survival – 60%, subadult survival - 80%), except where simulations were carried out to assess the impact of mass mortalities on population viability and where the impact of errors in estimates of adult and 1st-year survival on population predictions were examined. Because pre-breeding survival was applied to all pre-breeding age-classes, but error estimates only apply to the average yearly survival up to four years, the sensitivity of this parameter to population predictions under stochastic conditions was not considered.

Breeding Success: Data on annual breeding success (fledglings.pair^{-1}.year^{-1}) were pooled for sites and for pairs to give three data sets constituting the average number of fledglings.pair^{-1}.year^{-1} for each defined population (see also Ch. 3). Data sets thus defined for protected (25 site-years) and unprotected (57 site-years) mainland populations are extensive. These data did not differ significantly from normality for

either unprotected populations (KS test, Lilliefors Probs.; n=57, D=0.151, P>0.05) or protected populations (KS test, Lilliefors Probs.; n=25, D=0.127, P>0.05). However, for island populations, there are only 5 site-years of data (all from Dassen Island, off the west coast of South Africa) and, because of the nature of the more extensive data sets from mainland populations, normality was assumed. For the global population model, data on fledging success from the three defined populations were pooled: this data set also did not differ significantly from normality (KS test, Lilliefors probabilities; n=87, D= 0.12, P>0.05). For all defined populations, normal distributions were fitted to fledging success data and resultant distributions categorized into frequency histograms. Probabilities were applied to categories for fledging success defined in terms of intervals of 0.09 fledglings.pair^{-1}.year^{-1} and the mid-point (0.045 fledglings.pair^{-1}.year^{-1}) of each of these intervals was used to calculate the fledging success value for each category. The resultant normally distributed, categorical data sets on fledging success probability formed the input and basis of underlying variability in breeding success for stochastic population models applied to each of the defined populations. To initialise models under various scenarios, mean values for fledging success were used. This gave the following input (fledglings.pair^{-1}.year^{-1}) for each defined population: global population (0.40), island populations (0.91), protected mainland populations (0.42), and unprotected mainland populations (0.34).

Initial population numbers: Current estimates of total population sizes for islands (1941 individuals) and mainland (4729 individuals), based on surveys undertaken during the summer breeding season, were used as the basis for initial population numbers (Ch. 2). However, these counts reflect number of birds >1 year old. Secondly, total mainland counts had to be split between areas defined as protected and those defined as unprotected. Thus, to initialise models for the various areas under the differing scenarios, the following procedure was undertaken.

Single island population: The ratio of breeding birds to non-breeding birds for island oystercatcher populations during the breeding season is not well known, although summer counts from Robben Island (Calf and Underhill 2002) and for Saldanha Bay island populations (Loewenthal & Hockey unpublished data) suggest that it is greater than 9:1. (Note that this ratio is based on the average number of island-reared non-

breeders that are physically present on islands during the breeding season. However, it appears that a much larger proportion of island-reared nonbreeders spend most of their time on the mainland from which they make forays to islands, presumably in an attempt to establish territories –Ch. 5. These island-reared non-breeders on the mainland had to be excluded from calculations in setting the initial size of mainland populations arising from mainland-reared birds –see below). However, the ratio of breeders to non-breeders on islands was assumed to be 8:1, representing something approaching a worst-case scenario. This gave an island population of 1552 breeders and 389 non-breeders. The model was then run until a stable non-breeding population was established (1725 individuals). Age-at-first-breeding under stable-state conditions was established at 7 yrs.

Separate mainland populations: The total population size for the mainland, based on mainland-reared birds was established by firstly calculating the number of island-reared birds present on the mainland (i.e. 1752-389 = 1336 individuals) and then subtracting 1336 individuals from the total mainland count based on recent survey data (4729 individuals) to establish a total mainland population (based on mainland-reared birds) of 3393 individuals. Based on the 23% of coastline covered by protected areas, the total mainland population was split between protected areas and unprotected areas in the same proportion, to give a total UMP of 2714 individuals and a PMP of 679 individuals. The UMP population was then initialised by running the model and varying age-at-first-breeding until the total population size reached a stable state of 2714 individuals. This gave an age-at-first breeding of 4 yr, a breeding population of 2107 individuals and non-breeding population of 607 individuals. Similarly, characterising the PMP gave a breeding population of 483 individuals, a non-breeding population of 196 individuals and an age-at-first breeding of 5 yr.

Separate UMPs and PMPs with a shared non-breeding population: The model was initialised using breeding populations of 2107 and 483 individuals for UMPs and PMPs respectively. This gave a shared non-breeding population of 1118 individuals and an age-at first breeding of 5 yrs.

Global population model: The recently estimated global oystercatcher population size of 6670 individuals >1 yr old was used as the basis for this model. Initialising gave a

breeding population of 4849 individuals and 1821 non-breeding individuals, and an age-at-first-breeding of 5 yrs.

Initial conditions for a varying proportion of the total island breeding population impacted by mass mortality: The total breeding population of 1552 was split according to ratio to be impacted and not impacted. In each case, the non-breeding population was established at 1725 individuals and age-at-first-breeding remained 7 yr, as with the single-island population model.

Simulations and viability criteria

Because natural variation in breeding success was incorporated into all simulations, all results were defined probabilistically because each outcome was unique (even when simulated perturbations weren't applied - e.g. Fig. 6.3). For all simulations a time horizon of 200 years was applied. Target times in population projections are arbitrary (Reed *et al.* 1998), and 200 years was chosen as a reasonable time frame, given the long-lived, slow reproducing nature of the species.

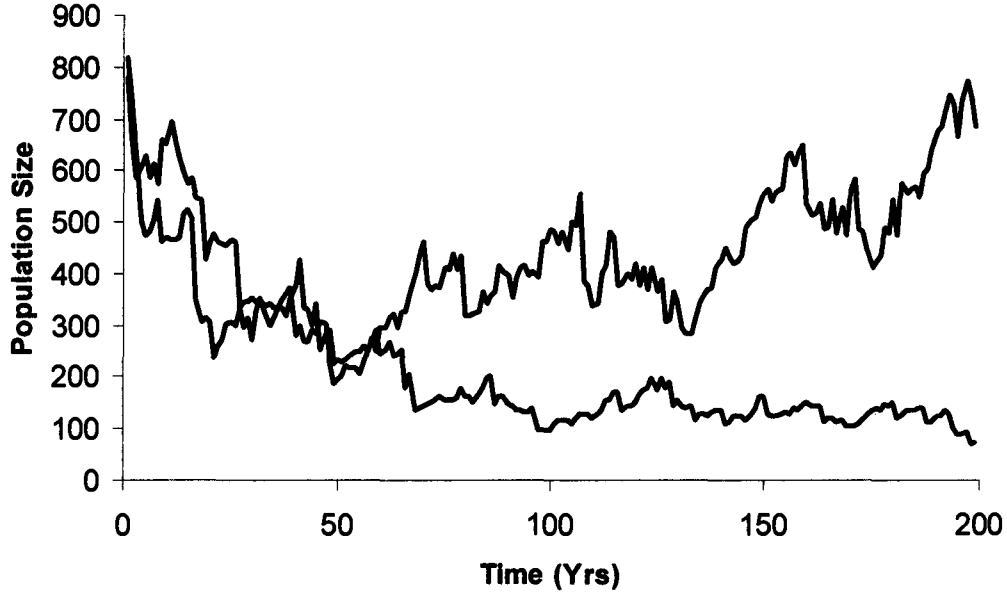


Fig. 6.3. Two possible population trajectories (total population size) based on simulations of a hypothetical, unprotected mainland oystercatcher population (see Methods). In both cases the parameters used are the same, but because fledging success is probabilistically modelled, two different outcomes are achieved. In this example adult survival =96%, 1st year survival= 60%, average yearly survival of one- to four-year old birds= 80% and fledging success is variable (see Methods).

Deciding on what constitutes a population as safe from extinction or not, is fraught with problems (Ludwig 1999) and meaningful estimates of extinction probabilities may only be possible for short-term time horizons (10% to 20% of the time over which the population has actually been monitored - Frieberg & Ellner 2000). Rather than make any *a priori* decision as to what constitutes an extinction probability for oystercatcher populations, two arbitrary criteria were used as yardsticks against which an assessment of population persistence was made – the probability of the population persisting at >50% of the initial population size and >5% of the initial population size. For all treatments 1000 simulations were carried out to establish probabilities and these were treated as sample distributions in cases where statistical comparisons were applied. One thousand simulations for each treatment generated sample distributions that could be compared using parametric statistics.

Comparison of population outcomes

Population definitions: Statistical comparisons of population outcomes were made for the following defined populations: (1) global population vs three separate sub-populations (2) two completely separate mainland populations vs two separate mainland breeding populations with a shared non-breeding population (3) between the three island scenarios, in terms of the proportion of birds impacted by stochastic events.

Survival parameters and population outcomes: The effect of error in estimates of first year survival and adult survival were assessed by statistically comparing population outcomes for mean ± SD values for these parameters, for UMPs, PMPs and IPs.

Perturbation simulations

There is great uncertainty as to the extent, severity and frequency of mass mortalities in oystercatcher populations. For each of the defined populations (UMP, PMP and IP) both the severity and frequency of mass mortalities were varied. In all cases, the frequency was modelled probabilistically as a 1-in-X year event. For both scenarios where the severity of mass mortalities was varied and where the frequency of mortalities was varied, only the survival of adult breeders was reduced.

Based on very limited knowledge, episodic events mentioned in the introduction to this chapter appear to have removed between 30% and 50% of adult breeding populations on the islands concerned (Hockey and Cooper 1980, D. Loewenthal pers. obs.). Where the frequency of mass mortalities was varied, the severity was fixed at 30%. Where the severity was varied, the frequency was probabilistically modelled as a 1-in-10 year event (again, this choice of frequency is somewhat arbitrary – and is based on the fact that two 'significant' mass mortalities have been observed between 1978 and 2000 (see Introduction). Little is known as to whether or how severely non-breeding oystercatchers may be subject to mass mortalities, since the vagility of the non-breeding population makes accurate counts (and hence detection of rapid population decreases) impossible. Non-breeding Eurasian Oystercatchers *H. ostralegus* in Europe are known to suffer large-scale mortalities, due mostly to severe weather (Goss-Custard *et al.* 1982) and this is an important factor influencing their population dynamics (Goss-Custard *et al.* 1996). For African Black Oystercatchers, there are no comparable large-scale environmental perturbations impacting non-breeding birds. However, given that a large proportion of the non-breeding population gathers in dense concentrations at localised areas and for extended periods of time (Hockey *et al.* 2003, Rao 2005), it may well be that they are subjected to the same episodic events impacting adult breeding populations. A third scenario was therefore considered, where both adult breeders and subadults (birds >1 year) were subjected to mass mortalities (with a 1-in-10 year probability) with increasing severity. In all the latter simulations, reductions in adult breeder survival and non-breeder survival were applied to the entire population. Clearly, this is an unrealistic scenario, since all available data indicate that adult mass mortalities are likely to be localised phenomenon (see Introduction). However, given the unpredictability of these events, in terms of locality and extent, such perturbations were applied to entire populations as a worst-case-scenario. In all cases where the impacts of varying the frequency and/or severity of mass mortalities was not explicitly being addressed, mass mortalities for island populations were modelled as events with a 1-in-10 year probability and reducing adult survival from 96% to between 50% and 70%-as the default option (this based on the severity and frequency of the two mass mortalities that have actually been observed on the Saldanha Bay Islands). As with all other mass mortality simulations, the probability of a particular severity was modelled as a flat distribution – thus a mass mortality event was equally

likely to reduce survival to 50% as opposed to 70%, or any other value between these extremes. Mainland populations were not subjected to mass mortalities, as the default option. For the scenario where the proportion of the island population impacted was varied, the severity of the perturbation regime was varied from a 10% reduction in adult survival up to a 90% reduction in adult survival: in all cases the frequency of a reduction in adult survival was kept constant, with a 1-in-10 year probability.

RESULTS

λ values

The relatively high inter-annual variation in breeding success of mainland African Black Oystercatcher populations had a predictably larger impact on the intrinsic growth rates for both UMPs and PMPs, than for IPs. In the case of UMPs, a reduction of one standard deviation in the average fledging success resulted in a negative population growth rate (Table 6.1).

Table 6.1. Natural variation in fledging success of African Black Oystercatchers and resultant intrinsic growth rates for populations. Population growth rates were calculated, based on deterministic models of oystercatcher population dynamics using the parameters of fledging success, adult, subadult and 1st year survival, age-at-first-breeding and longevity.

	Fledging success (fledglings.pair^{-1}.year^{-1})			λ (Intrinsic population growth rate expressed as %)		
	- 1 SD	Mean	+1 SD	-1 SD	Mean	+1 SD
Islands	0.78	0.91	1.04	15.4	17.5	19.4
Protected mainland	0.23	0.42	0.61	3.0	7.6	11.2
Unprotected mainland	0.10	0.34	0.58	**-2.1**	6.4	11.8

The fact that a reduction of 1 SD in fledging success could switch the intrinsic growth rate of UMPs from positive to negative provided a further rationale to use stochastic models incorporating this demographic stochasticity. As expected for a

long-lived species with a relatively large adult breeding population, the intrinsic growth rate of all populations was very sensitive to variation in adult survival. However, the relatively small error in the estimate of this parameter resulted in little absolute variation in intrinsic growth rates for all three populations (Table 6.2). The

Table 6.2. Variation in the estimate of adult survival (to the nearest %) and resultant intrinsic growth rates for oystercatcher populations. Population growth rates were based on deterministic matrix models of oystercatcher population dynamics using the parameters fledging success, adult, subadult and 1st year survival, age-at-first-breeding and longevity.

	Adult survival			λ (Intrinsic population growth rate expressed as %)		
	-1 SD	Mean	+1 SD	-1 SD	Mean	+1 SD
Islands	94	96	98	16.2	17.5	18.8
Protected mainland	94	96	98	6.4	7.6	9.0
Unprotected mainland	94	96	98	4.9	6.4	7.9

large error in the estimate of 1st-year survival had a relatively small influence on the intrinsic growth rate of all three populations (Table 6.3). By contrast, increasing the

Table 6.3. Variation in the estimate of 1st year survival (to the nearest %) and resultant intrinsic growth rates for oystercatcher populations in the areas given. Population growth rates calculated, based on deterministic models of oystercatcher population dynamics and using parameters on fledging success, adult, subadult and 1st year survival, age-at-first breeding and longevity.

	1st-year survival			λ (Intrinsic population growth rate expressed as %)		
	-1 SD	Mean	+1 SD	-1 SD	Mean	+1 SD
Islands	45	60	75	13.8	17.5	20.8
Protected mainland	45	60	75	5.3	7.6	9.7
Unprotected mainland	45	60	75	4.0	6.4	8.5

age-at-first breeding from 4 yr to 10 yr for the IP had a large impact on the intrinsic growth rate, nearly halving its value from 17.5% to 9.5% (Table 6.4).

For mainland populations, even increasing the age-at-first breeding by 2 years had a relatively large influence on λ. Both PMPs and UMPs were equally sensitive to an increase in age-at-first breeding (with λ decreasing by *ca* 2% - Table 6.4).

Table 6.4. The effect of varying age-at-first-breeding on the intrinsic population growth rate. Values for age-at-first breeding based on maximum and minimum known values for oystercatcher populations in the areas given. Population growth rates calculated, based on deterministic models of oystercatcher population dynamics and using parameters on fledging success, adult, subadult and 1st year survival, age-at-first breeding and longevity

	Age-at-first-breeding		λ (Intrinsic population growth rate expressed as %)	
	Min.	Max.	(Min. age-at-first-breeding)	(Max. age-at-first breeding)
Islands	4	10	17.5	9.5
Protected mainland	4	6	7.6	5.9
Unprotected mainland	4	6	6.4	4.8

Existing error (± 1 SD) in the estimate of average yearly survival for birds between one and four years old had a relatively small impact on λ for all populations (Table 6.5).

Table 6.5. Variation in the estimate of average yearly survival for oystercatchers, between the age of 1 and 4 yrs old, and the impact on the resultant intrinsic growth rate of oystercatcher populations in the given areas.

	Average survival from 1-4 yr			λ (Intrinsic population growth rate expressed as %)		
	-1 SD	Mean	+ 1 SD	-1 SD	Mean	+ 1SD
Islands	72	80	88	14.7	17.5	20.3
Protected mainland	72	80	88	5.9	7.6	9.4
Unprotected mainland	72	80	88	4.6	6.4	8.2

Stochastic model simulations

Comparisons of different population types and model structures

There was a significant difference (after 200 years) for oystercatcher populations treated as one entity vs. populations treated as three separate entities ($t_{(2),1998} = 9.78$,

$p<<0.001$), providing a rationale for considering three separately defined populations in subsequent analyses.

Comparison of the two defined mainland populations (shared non-breeding population vs. completely separate populations) also indicated a significant difference in the population outcome for the total mainland population: in the case where breeding populations shared a floater population this resulted in a greater total mean population size at 200 years ($t_{(1),1998}=3.38$, $p<0.001$). Thus permanent movement of birds from protected mainland populations to unprotected mainland populations may be important in improving the persistence probability of (intrinsically unsustainable) breeding populations on the mainland and provides some rationale for further investigation into the degree of connectivity between different breeding populations on the mainland (particularly in light of future increased fragmentation of breeding populations due to coastal development).

Fig. 6.4. Graph illustrating the effect of simulated mass mortalities of breeding adult oystercatchers, on the total island population (IP) after 200 years. The severity (90% reduction in the survival of breeding adults) and probability (1-in-10 years) is kept constant while the proportion of the breeding population affected is varied. Box and whiskers represent mean ± 1 SD values: each is based on 1000 simulations.

Simulations where the ratio of impacted to non-impacted breeding populations, and the severity of mass mortalities were varied, showed that even under conditions of severe mass mortalities (90% reduction in adult survival), island populations were still very resilient to these impacts (even when 75% of the breeding population was impacted). Predictably (given the severity of simulated mass mortalities where a 90% reduction in adult survival was effected), varying the proportion of impacted breeding island birds (with a shared non-breeding population)

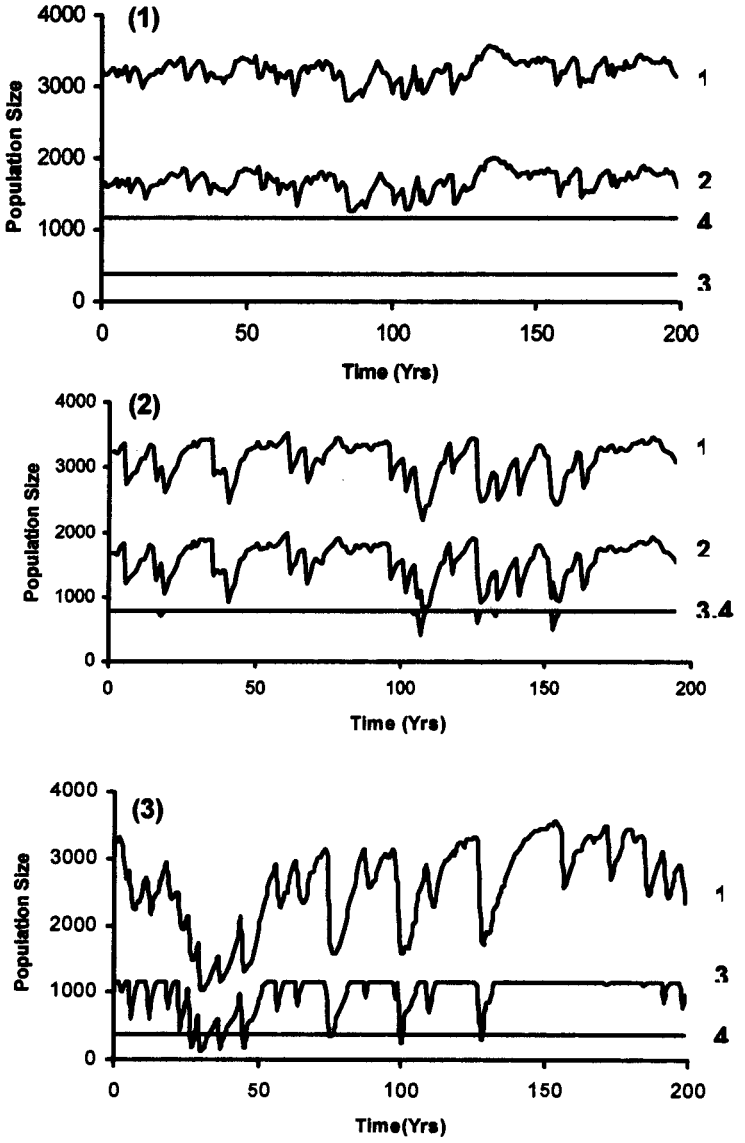


Fig. 6.5. The effects of adult mass mortality simulated over 200 years for island populations sharing a common non-breeding population (see text). The severity (90% reduction in adult survival) and frequency (1-in-10 yr probability) is the same in each scenario, but the proportion of the breeding population affected varies from 25% (1) to 50% (2) and finally to 75% (3). In each case, plots 1, 2, 3 and 4 respectively represent the total population, the non-breeding population, and the affected and unaffected proportion of the breeding population. In (3) above, the trajectory of the non-breeding population has been excluded, for clarity of presentation.

between values of 25% and 75%, significantly influenced population size ($F_{2, 2997}$ = 276, p <0.001). However, visual inspection shows that despite the large change in the proportion of the island population impacted, and the severity of the perturbation regime imposed (90% reduction in adult survival with a 1-in-10 year probability), the shared non-breeding population effectively buffered breeding populations against the impacts of these events: the mean population size at 200 years only decreased from *ca* 3200 to *ca* 2700 individuals despite the impacted to non-impacted proportion of the population being increased from 25% to 75% (Fig. 6.4). Even when 75% of the island population was impacted, the non-impacted breeding population did not decrease over 1000 simulations – the non-breeding population was thus more than large enough to replace losses from both impacted (through stochastic events) and non-impacted (mortality occurring naturally) breeding populations: Fig. 6.5 illustrates a typical 200 yr simulation run for each scenario.

Impacts of variability in estimates of adult and 1st year survival

Varying 1st-year survival between three distinct values (mean ± 1 SD) for UMPs and PMPs indicated that error in the estimate of 1st-year survival had a significant impact on the population outcome, both for UMPs ($F_{2, 2997}$ = 27681, p<<0.001) and for PMPs ($F_{2, 2997}$ = 22171, p<< 0.001). However, the population outcome for the IP was not significantly affected by such error ($F_{2, 2997}$ = 1.256, p = 0.285). The reason for the lack of impact of varying 1st year survival, on island populations, is probably that the severe mass mortality regime applied (as a default) to island populations 'swamped' the effect of varying 1st year survival. Not only was the mass mortality regime severe (modelled as a 30 to 50% reduction in adult survival across the entire island population, with a 1-in-10-year probability), but because mass mortalities were modelled as reductions in the survival rate, increases in the adult population (due to an increase in 1st year survival) resulted in an increase in the impact of mass mortalities in terms of absolute numbers, thus effectively dampening the potential increase in the mean total population size due to improved 1st year survival. (The implications of modelling mass mortalities as reduction in adult survival rates-rather than absolute numbers-is further considered in the discussion to this chapter).

Visual inspection of the results indicates that for PMPs, varying 1st-year survival between 75% and 45% resulted in a fairly even decrease in the population size at 200 years. For the UMP, by contrast, there was relatively little change in the

resultant population size when 1st-year survival was reduced from 75% to 60%, but when survival was further decreased from 60% to 45%, the total population size was reduced from >2500 individuals to slightly more than 500 individuals (Fig. 6.6).

Varying adult survival in the same way as for 1st-year survival (mean ± 1 SD) resulted in all three populations being significantly affected: UMP ($F_{2,2997}$ = 11 709, p<<0.001); PMP ($F_{2, 2997}$ = 431, p << 0.001); IP ($F_{2, 2997}$ = 302, p<<0.001). Visual inspection indicated that for UMPs, there was a sharp decrease in population size when adult survival was reduced from the mean to – 1 SD (Fig. 6.7).

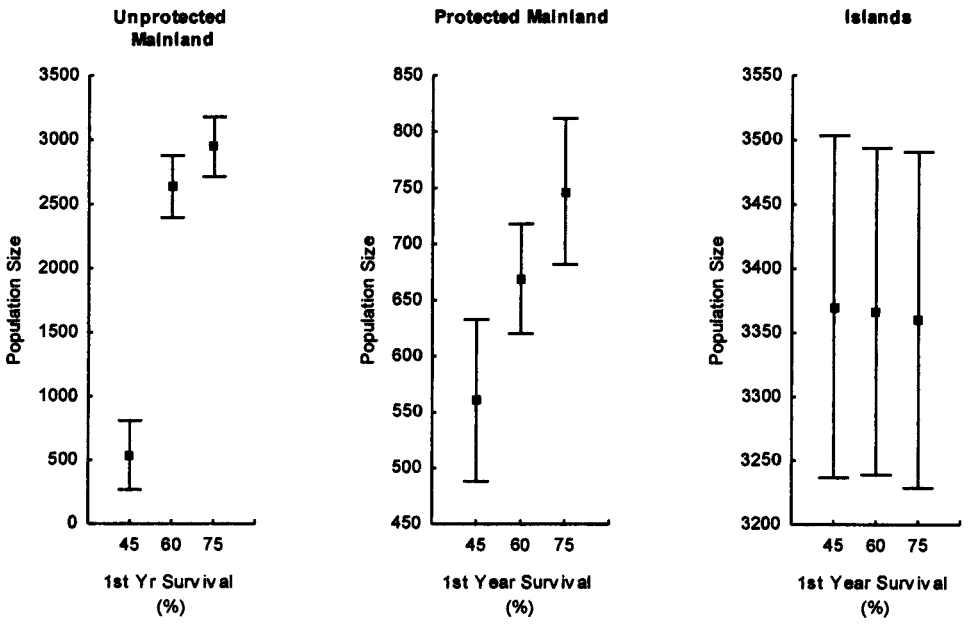


Fig. 6.6. The effect of varied 1st year survival rates on population outcomes at 200 years. Box and whiskers represent mean ± 1 SD values and are based on 1000 simulations for each scenario.

Simulated mass mortalities

For a simulated mass mortality on islands, occurring with a 1-in-10- year probability, the results suggest that adult survival would have to be reduced by ca 60% before there was any risk of the population being reduced below 50% of the original carrying capacity (K) within 200 years. Even if the adult breeding population was removed completely, with the same mass mortality probability, there was still some (although small) chance of persistence. Mainland populations were much more sensitive to

simulated mass mortalities: for PMPs a reduction in adult survival of 20% would reduce the probability of population persistence above 50% of the initial carrying capacity (Fig. 6.8). UMPs would be affected at the 50% level, with a reduction in adult survival of <10% occurring with a 1-in-10-year probability. A 50% and 40% reduction in adult survival (also with a 1-in-10-year probability) for PMPs and UMPs respectively would likely eliminate populations (Fig. 6.8). For all defined populations, once the persistence probability of the population above 50% of original K was impacted due to a reduction in adult survival, the persistence probability rapidly decreased with any further reduction in adult survival (Fig. 6.8). Furthermore, for all defined populations, once the persistence probability at the 50% level was reduced, the persistence probability at 5%K also began to decrease rapidly with a relatively small further reduction in adult survival (Fig. 6.8).

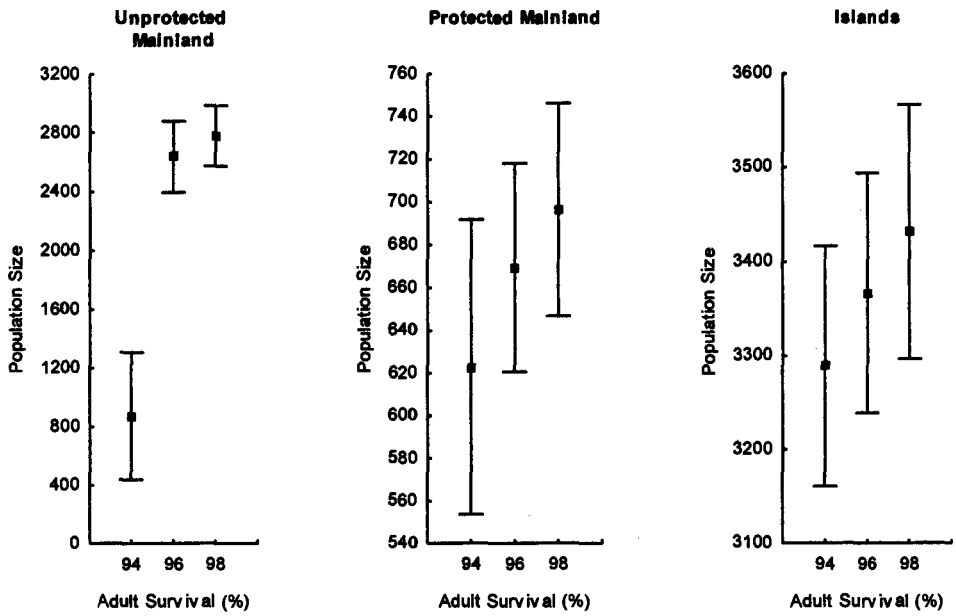


Fig. 6.7. The effects of varied adult survival on population outcomes at 200 years. Box and whiskers plots represent mean ±1 SD values and are based on 1000 simulations for each scenario.

A 30% reduction in adult survival would only start to the impact the persistence probability of the IP at 0.5K when the frequency of the event had a probability of.

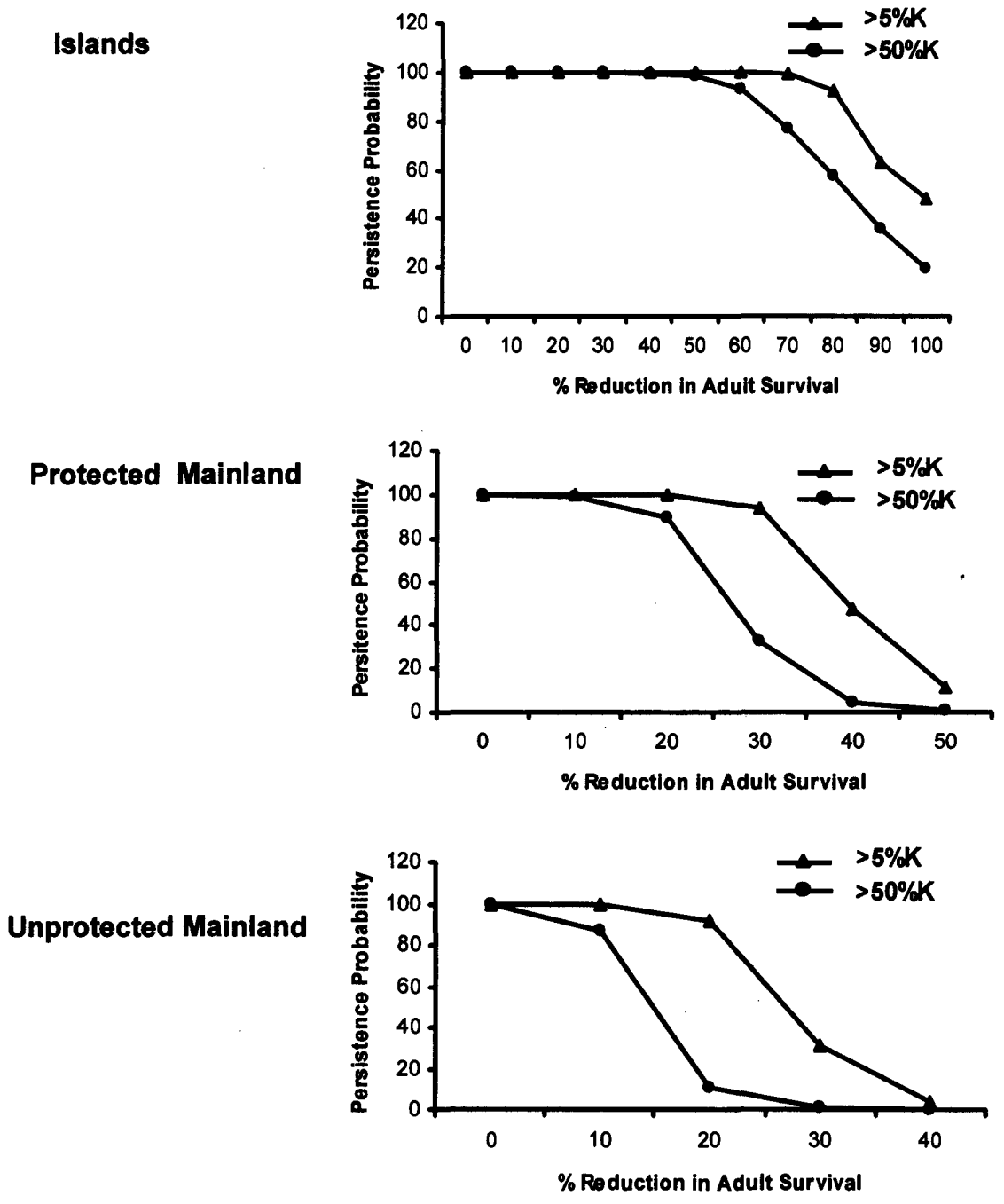
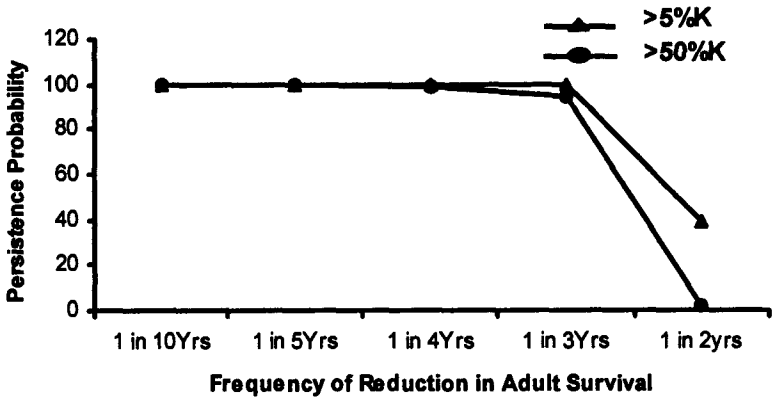
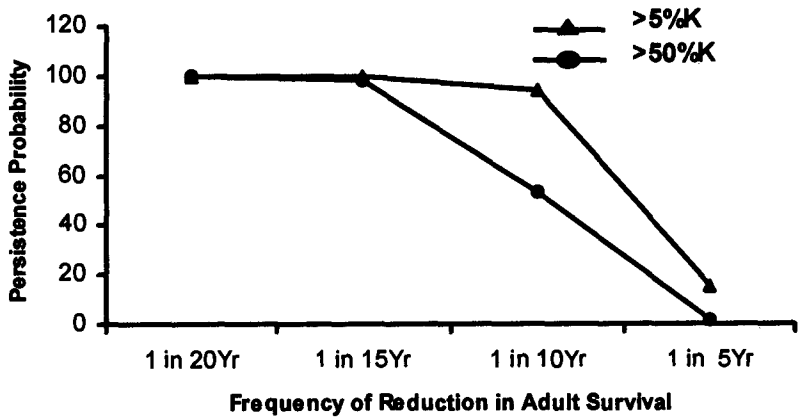


Fig. 6.8. Probability of population persistence over 200 years with an increase in adult mass mortality. In all cases severity is expressed as a % reduction in adult survival rates with a 1-in-10 year probability. Triangles and circles represent the probability of the population persisting at >5% and >50% of the original carrying capacity, respectively. Probabilities are based on 1000 simulations.

Islands



Protected Mainland



Unprotected Mainland

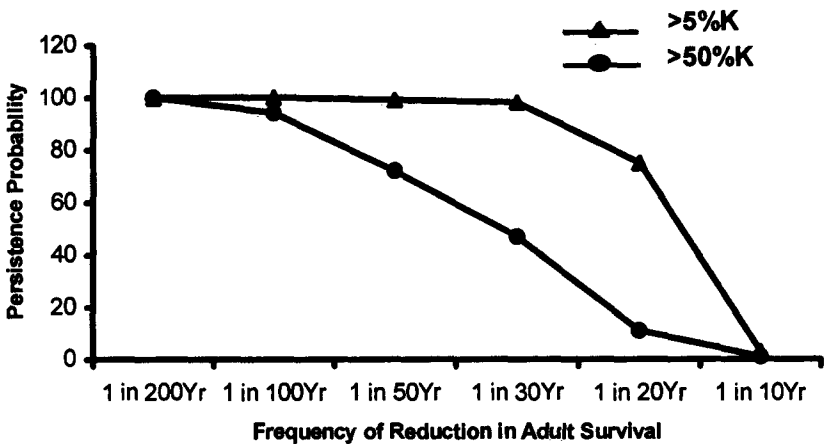
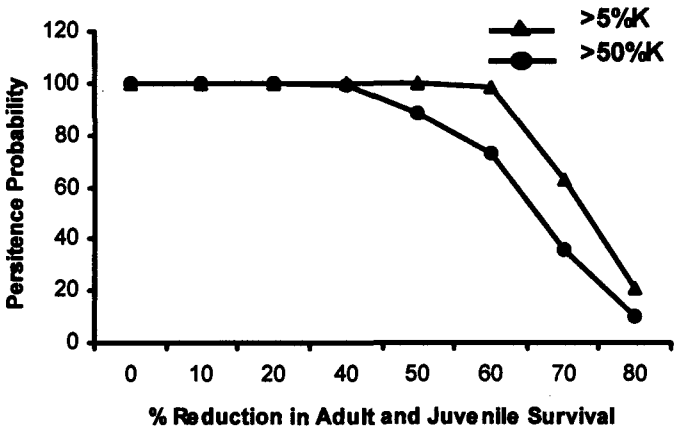


Fig. 6.9. Probability of population persistence over 200 years with an increase in the frequency of simulated adult mass mortalities. In all cases, severity is expressed as a fixed 30% reduction in adult survival rate with a varying probability of occurrence. Probabilities are based on 1000 simulations.

Islands



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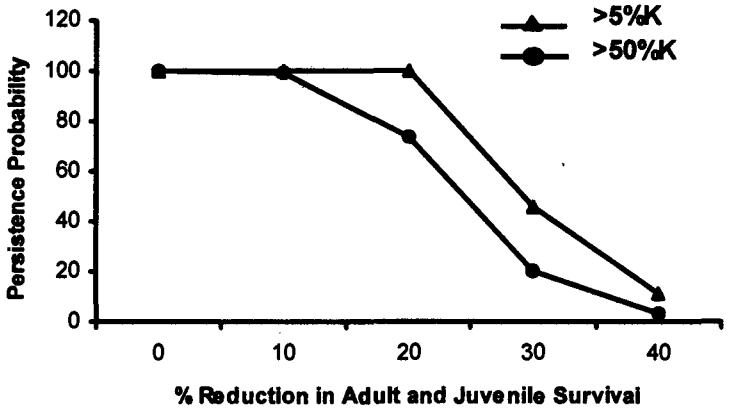

Unprotected Mainland

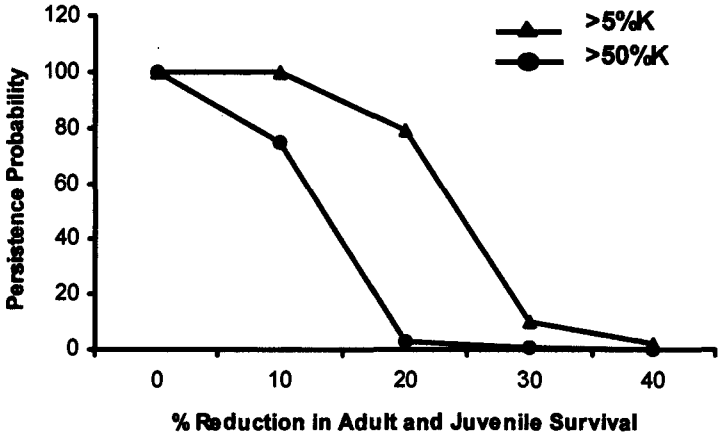

Fig. 6.10. Probability of population persistence over 200 years with an increase in adult and subadult (1-4-year old) mass mortalities. In all cases severity is expressed as a % reduction in mean adult and juvenile survival rates with a 1-in-10 year probability of occurrence.

occurrence of 1-in-3-years: if the probability increased to 1-in-2-years, the likelihood of population persistence was very rapidly reduced. For PMPs, a simulated mass mortality with a 1-in-15-year probability would begin to impact the population at the 0.5K level, while a 1-in-5-year probability of occurrence would likely cause extinction. For UMPs, even an event where adult survival was reduced by 30% and occurring with a 1-in-50 year probability noticeably reduced the persistence probability of the population at 50%K, while 1-in-10 yr occurrence with the same severity would likely lead to extinction (Fig. 6.9).

Simulated mass mortalities of both adult and non-breeding populations indicated that mass mortalities of non-breeders had a relatively small effect on population persistence for all scenarios (cf Figs. 6.8 and 6.10). However, relatively speaking, there was an increasing sensitivity to non-breeder mass mortality, moving from UMPs to PMPs and finally to IPs (cf. Figs. 6.8 and 6.10). For example, in the case of UMPs, a 10% reduction in adult survival, as opposed to a 10% reduction in both adult and subadult survival, only changed the persistence probability at 50%K, by *ca* 5%. In the case of IPs, a much greater reduction in survival rates was required to reduce persistence probability at the 50% level. However, as a comparative example, a 60% reduction in just adult survival compared to a 60% reduction in both adult and subadult survival for island populations, resulted in a difference in persistence probability at 50%K, of *ca* 20%.

DISCUSSION

Intrinsic growth rates

Despite life-history traits predicted to promote relatively low population growth – i.e. relatively low fecundity, late maturity and high longevity - this study suggests that, under favourable circumstances, the African Black Oystercatchers *Haematopus moquini*, is capable of extremely rapid population growth rates as evidenced by the very high λ values for island populations. This situation is not unique to *H. moquini* and, under favourable conditions, extremely high reproductive success and rapid population growth rates have been observed for both Eurasian Oystercatchers (Harris & Wanless 1997) and American Black Oystercatchers *H. bachmani* (Gill *et al.* 2004). While the λ values for island populations in this study are based on breeding success data from Dassen Island only, breeding success is almost certainly comparably high

on other west coast islands. Even on Robben Island in Table Bay, which is subject to human disturbance and has terrestrial predators, average fledging success over one season was calculated as 0.74 fledglings.pair^{-1} (Calf & Underhill 2002). Conditions on islands off the west coast of South Africa are ideal for African Black Oystercatchers. In most cases there is a lack of terrestrial predators, a rich food supply and a high degree of protection (Ch. 2). Evidence that the high intrinsic island population growth rates predicted here have translated into relatively large population increases, come from long term data sets from Jutten Island and Malgas Island in Saldanha Bay. Populations at these islands have virtually doubled since the 1980s, due to a combination of protection, lack of terrestrial predators and an improved food supply (in the form of the invasive mussel *Mytilus galloprovincialis*): these populations have been stable for several years and are now almost certainly at carrying capacity (Ch. 2). Oystercatcher numbers at Dassen and Robben Islands in the Western Cape have also increased markedly (Ch. 2). Intrinsic growth rate for PMPs was estimated to be less than half that for islands and for UMPs are even lower. Given the variation in breeding success at all sites, this suggest negative growth potential for some areas, especially UMPs. This is reflected in population changes on the mainland where, despite improved food supply due to the invasive mussel *Mytilus galloprovincialis*, population increases have been much lower and, at 41 of 239 study sites on the mainland, population decreases have occurred (Ch.2).

The intrinsic population growth rate is an important parameter in conservation as it provides an indication of firstly the robustness of populations to environmental perturbations, and secondly a population's recovery potential. Furthermore, understanding how various components of the demographics of a population affect λ is important in improving the growth potential of populations through management (Heppel & Crowder 1998, Heppel *et al.* 2000). Across a broad range of avian taxa the influence of the fecundity rate on λ increases with a decrease in adult survival rate, while in long -lived species that mature late and lay few eggs, adult survival rate makes the greatest contribution to λ (Saether & Bakke 2000). African Black Oystercatchers fall into the latter category and λ values were certainly more sensitive to changes in adult survival than to changes in fecundity. For example, in island populations (Tables 6.1 and 6.2), varying adult survival by 4% (i.e. by $\pm$ 1 SD) resulted in a 16% change in λ, whereas a 26% change in fledging success ($\pm$ 1 SD) produced only a 26% change in λ. However, despite the higher sensitivity of λ to adult

survival, as opposed to fledging success, the real variation in fledging success (both annually and between sites) observed in oystercatcher populations is so large that it is having an overriding impact on the population growth rates of *H. moquini*.

Considerable variation in both site-related and inter-annual fledging success, is reported for several other oystercatcher species (Newman 1992, Hockey 1996, Davis *et al.* 2001, Hazlitt and Butler 2001, Sagar *et al.* 2002, McGowan 2005). Fledging success of *H. moquini* on islands is more than double that for PMPs and nearly triple that for UMPs (Table 6.1). Based on the matrix projection model used here, the critical fledging success required to produce an intrinsically sustainable population is 0.28 fledglings.pair^{-1}.year^{-1}. Currently, in UMPs, the average fledging success is only marginally higher than this, at 0.34 fledglings.pair^{-1}.year^{-1} and, as indicated by the variance, is frequently below 0.28 (Table 6.1). Given that variation in fledging success is considerable and fluctuates both above and below sustainable levels, the pattern of variation, particularly in UMPs, warrants further investigation. Current data suggest that inter-annual variation in fledging success is normally distributed (and this pattern of variation provided the input for the stochastic simulation models presented in this chapter). The intrinsic growth rate was also found to be relatively insensitive to 1st-year survival. For example (Tables 6.1 and 6.3), a 67% change in 1st-year survival (± 1 SD) produced a 50% change in λ, whereas the 4% change in adult survival produced a 16% change in λ.

However, real error in the estimate of 1st-year survival has an overriding influence on λ. This error arises from currently large uncertainty as regards resighting probability vs survival probability of colour-ringed juvenile oystercatchers in statistical estimation of the latter parameter (D. Loewenthal and P.A.R. Hockey unpubl. data). However, juvenile oystercatchers are largely confined to specific roost sites (Rao 2005) and continued colour ringing of juvenile oystercatchers and increased observer effort at these roost sites should make it possible to refine this estimate in the future.

The influence of variation of the age-at-first breeding on the intrinsic growth rate (Table 6.4) also warrants further investigation into the pattern of recruitment of pre-breeding oystercatchers into adult breeding populations. Current evidence from colour- ringed birds recruiting into the breeding populations on Saldanha Bay Islands points to delayed reproduction and age-based recruitment (at least between 4 and 10 years of age – Ch. 5). λ values presented here are measures of long-term, stable (i.e.

asymptotic) growth rates. However, environmental disturbances may significantly alter population states (i.e. age-at-first-breeding, age distribution) and empirical evidence suggests that stable population states rarely occur in nature (Bierzychudek 1999, Clutton-Brock & Coulson 2002). Further, comparisons of long-term and short-term population dynamics for a wide range of species (Koons *et al.* 2005) indicate that for long-lived, slow-reproducing species, variability in transient population dynamics and differences between populations characterised by being in stable or unstable states, are likely to be greater than for short-lived, fast reproducing species. African Black Oystercatchers have life-history traits characterised by high longevity, low reproductive output and late maturation. Furthermore transient African Black Oystercatcher populations (i.e. populations that are between stable states) are likely to be widespread, particularly on the mainland where populations have been and currently continue to be influenced by changes in habitat quality – and particular, an improved food supply due the invasion of the alien mussel *Mytilus galloprovincialis* and due to protection (Ch. 2, Ch. 7). (On the offshore islands considered in this study, it appears that (at least) breeding oystercatcher populations have reached a stable upper limit, having increased previously in response to both protection and an improved food supply-see Ch. 2, Ch. 7). These considerations warrant future investigation into how changes in environmental quality mentioned here are impacting on oystercatcher population dynamics, and if so, to what degree this may affect long-term predictions of population size. (in this study, a start has been made to understand how local oystercatcher populations respond to changes in habitat quality-Ch. 7). Recent studies suggest that consideration of transient population dynamics can significantly affect long-term population predictions (Koons *et al.* unpublished data, cited by Koons *et al.* 2005).

Stochastic models and viability analyses

The large error in estimates of 1st-year survival, and its impact on the population outcome at – 1 SD for UMPs, further highlights the need to try and refine this parameter. In general, the low reproductive success of mainland oystercatcher populations makes them the most sensitive to variation in 1st-year and adult survival.

Assuming all populations are closed, then model initialisation suggests that, despite the smaller size of breeding populations on islands, the reservoir of non-breeders available to replace lost breeders is far larger (due to the much higher

reproductive output of birds on islands) than that for both mainland populations. Thus, in the face of mass adult mortalities, island populations are at an advantage, both due to a higher reproductive success, and a larger accumulated pool of non-breeders. Empirical evidence that the large predicted pool of island-generated non-breeders does indeed exist comes from the two occasions when mass mortalities were observed. In 1978, after an episode of Paralytic Shellfish Poisoning, even though breeding numbers were virtually halved, they had all but recovered one year later (Hockey & Cooper 1980). In 1999, populations of oystercatchers on Jutten Island and Malgas Island were reduced by approximately 30% -almost certainly as a result of an avian cholera outbreak (Ch. 2) - but had recovered to pre-mass mortality levels by the following breeding season.

Models suggest that IPs are extremely well buffered against the impacts of episodic mass mortalities - even if both breeding and non-breeding populations are impacted. Given current levels of breeding success and an extensive reservoir of non-breeders, mass mortalities would be highly unlikely to pose a threat to the viability of IPs. Furthermore, island populations could withstand mass mortalities of present-day magnitude at far higher frequencies than is currently the case.

The low breeding success and relatively small reservoir of non-breeders on the mainland potentially make mainland populations more vulnerable than island populations to the impacts of mass mortalities. For example, a 20% reduction in adult survival with a 1-in-10-year probability would considerably reduce the persistence probability of UMPs. However, simulations applied here assume that the entire breeding population is impacted. Mass mortalities occurring with a 1-in-10-year probability are highly unlikely to impact breeding populations on the mainland at this scale, but may have severe local impacts as has been the case on islands. Further, although simulation models of mass mortalities on the mainland assume no connectivity between non-breeding populations, there is evidence for some connectivity in this regard (Ch. 5). Connectivity between impacted and non-impacted populations is likely to make a considerable difference to viability of oystercatcher populations as evidenced by simulations of severe mass mortality for island populations with a shared non-breeding population (Figs. 6.4 and 6.5). Estimates of mean population size at 200 yrs for PMPs and UMPs combined, with and without a shared non-breeding population were also significantly different, even in the absence of simulated mass mortalities.

Models presented here further assumed no connectivity in terms of non-breeding populations, between island and mainland populations. This assumption appears to be well supported (Ch. 5).

Taken together, results of these simulations suggest that, both for mainland populations and island oystercatcher populations, episodic events of the frequency and magnitude that are known from limited records, would certainly not be sufficient to precipitate a global extinction. Models presented here consider unified, single populations for each of UMPs, PMPs and IPs. However, in reality PMPs are nested within a matrix of UMPs – and IPs comprise numerous smaller island populations. Oystercatchers are known to display extremely high natal site philopatry, to the point where juvenile birds return almost exclusively to their natal islands. There is also some, although limited, data indicating that the level of natal site philopatry is also very high for mainland oystercatcher populations, but currently, a lack of data means that there is still a large degree of uncertainty as to the extent and level of natal philopatry for local oystercatcher populations on the mainland. (Ch. 5). Furthermore, models used in this study are unlikely to be well equipped to assess the impacts of many forms of environmental stochasticity, on small localised populations: they describe mass mortalities by a reduction in adult survival – thus (in model simulations) small populations can never be extirpated –only reduced to a state of near-extinction. The way in which mass mortalities was modelled, is therefore likely to underestimate the impact (in terms of population numbers) of these events, at small population sizes because as the population size decreases, the impact, in terms of numbers of individuals also decreases. While the impact of mass mortalities due to disease (e.g. such as the spread of avian cholera through a population) may well be dependent in some way on population densities, PSP, for example, will act independently of population size and hence may have a much more severe impact on small and localised populations, than models used here predict.

Given that severe episodic mass mortalities are know to occur at a local scale, and mainland populations have much lower reproductive potential than island birds, it is conceivable that local near-extinction of populations may be precipitated through episodic events such as PSP. Increased coastal development has resulted in population decreases at numerous sites on the mainland of South Africa (Ch. 2). While these declines more than likely often simply reflect movement of birds to other areas of more suitable habitat, the long-term effect of increased coastal development in terms

of fracturing the mainland population into more numerous and more isolated fragments may be of much greater future concern. Increased fragmentation and isolation of local oystercatcher populations may increase the future vulnerability of local populations to both environmental stochasticity (i.e. PSP outbreaks, avian etc.) and (given the high variability in breeding success, often below sustainable levels in current UMPs) to the negative effects of demographic stochasticity at low population numbers (Gilpin & Soulé 1986). These concerns warrant further investigation into the degree of connectivity between local oystercatcher populations on the mainland of South Africa.

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CHAPTER 7

POPULATION REGULATION, COMPETITIVE ASSYMETRIES, AND THE NATURE OF TERRITORIALITY: FINDINGS BASED ON A STUDY OF OYSTERCATCHERS *HAEMATOPUS MOQUINI*

INTRODUCTION

Territoriality is widespread in monogamous birds (Lack 1968, Davies 1978). Benefits of defending a territory may include sole access to resources (for example foraging and nesting/chick-rearing habitats), mate guarding and lowered predation risk (Davies 1978, Davies & Houston 1984, Carpenter 1987a, Carpenter 1987b, Møller 1987, Davies 1991, Sutherland 1996, Newton 1998). In oystercatchers, territory defence is considered essential for access to and exclusive use of resources such as nesting habitat, chick-rearing habitat and food (Ens 1992, Banks 1998). However, territory defence inevitably incurs costs (Brown 1969, Heppleston 1972, Safriel *et al.* 1984): for oystercatchers these costs usually include long periods of time involved in defence behaviours such as piping displays, ground and aerial chases and fights (Harris 1970, Baker & Hockey 1984, Ens 1992, Heg 1999).

Theory holds that the benefits of defending a territory must outweigh the costs in order for territoriality to be favoured by natural selection (Davies & Houston 1984). This does not preclude variation in territory sizes for a given resource density, but natural selection should favour birds that are able to defend a territory of a size that maximizes the difference between costs and benefits. If the latter condition holds, then an inverse relationship should be expected between territory size and resource density: this has been substantiated since at least the early 1970s (e.g. Gass *et al.* 1976).

Territoriality frequently precludes sexually mature birds from becoming breeders. This can be an important form of population regulation if the number of adults excluded from territories is large (Harris 1970, Ens 1992, Goss-Custard *et al.* 1995, Newton 1998, Heg 1999). Characteristics of populations regulated by territorial exclusion typically include rapid replacement of removed territorial pairs and the

presence of large numbers of birds near or adjacent to either prime breeding and/or feeding habitat (Newton 1998). The presence of large numbers of surplus birds attempting to acquire territories, but prevented from doing so, means that breeding populations comprising territorial individuals typically are tightly regulated, with some fluctuation from year to year, but with little real change in numbers, unless there is a change in habitat quality (Krebs 1970, Klomp 1980, Patterson 1980). Among Eurasian Oystercatchers *H. ostralegus* territoriality is primarily responsible for regulating breeding populations (Harris 1970), with many sexually mature birds in or adjacent to breeding grounds, but not breeding (Harris 1970, Safriel *et al.* 1984, Ens *et al.* 1995, Heg *et al.* 2000, Bruinzeel *et al.* 2004). Some of these 'floaters' are as old as 10 years (Ens 1992).

The African Black Oystercatcher *H. moquini* is less well studied, but two sources of evidence suggest territorial exclusion occurs. Firstly, there are a large number of birds fully capable of breeding but not doing so, mostly adjacent to but also within prime breeding habitat (Ch. 5). Some of these birds are at least seven years old but appear not to have bred. However, given that the colour-ringing study has only been running for seven years there may be nonbreeding birds much older than this. Secondly, although one, small removal experiment has been undertaken on the African Black Oystercatcher (in which pairs were rapidly replaced – P.A.R. Hockey unpubl. data), two much larger natural removal experiments of oystercatchers in prime breeding habitat strongly suggest that sexually mature birds are excluded in large numbers from high-quality habitats. In 1978, an outbreak of Paralytic Shellfish Poisoning (PSP) virtually halved populations on five islands off South Africa's west coast (Hockey & Cooper 1980), but these losses were replaced rapidly: one year later, populations were already at approximately 80% of pre-PSP levels (Hockey & Cooper 1980). Similarly, in 1999, populations on Malgas and Jutten Islands were reduced by approximately 30% (probably as a result of avian cholera – see Ch. 6), but numbers recovered in less than one year.

Other negative feedback processes that may be operating in African Black Oystercatcher populations can be grouped into two categories – mechanisms which regulate single populations (including territoriality) or mechanisms which regulate metapopulations (Rodenhouse *et al.* 1997). Most research on regulatory mechanisms in single populations has focused on negative feedback processes caused by local crowding (Sinclair 1989, Murdoch 1994). Among African Black Oystercatchers there

is evidence that reproductive output (measured as the ratio of one to two-chick broods) on two islands off the west coast of South Africa decreased over a *ca* seven-year period following increases in the breeding population (Ch. 2). At Goukamma Nature Reserve on the south coast of South Africa, however, the breeding population increased dramatically between the late 1980s and the mid 1990s, but there was no concomitant pattern of decreasing productivity (see Fig. 7.5). There is thus, at best, some evidence that density-dependent breeding success may play a limited role in population regulation, but this seemingly operates only at very high breeding densities, where exclusion of birds capable of breeding is already likely to be considerable.

Forms of population regulation related to metapopulation dynamics inevitably bring into question aspects of habitat heterogeneity and scale. In its most extreme form, this suite of regulatory mechanisms involves no accumulation of floaters, because previously excluded animals do not repeatedly try to force their way into the best quality habitats or wait for space to become available in these habitats. Rather, they move almost immediately to successively poorer quality habitats as the better habitats are filled. The tendency for settled birds to exclude unsettled birds underpins the Ideal Despotic Distribution (Fretwell & Lucas 1970) and is predicted to result in a situation where reproductive success is positively correlated with habitat quality, as has been amply demonstrated for *H. ostralegus* (e.g. Ens *et al.* 1992). Under this scenario, populations therefore cannot be regulated by density-dependent breeding success. Rather, regulation occurs because the average breeding success of the population is reduced as poorer-quality habitats are progressively occupied (Rodenhouse *et al.* 1997). In this form of regulation, often termed site-dependent regulation, the population will expand spatially as it grows. However, if the habitat quality gradient is very steep, population regulation can occur within a small area. For African Black Oystercatchers this is unlikely to be an important form of population regulation at a scale of tens of kilometres or greater because natal philopatry is very strong at this scale: among island-breeding populations birds return almost exclusively to their natal islands in an attempt to establish breeding territories (Ch. 5). However, even at a scale of kilometres or less, coastal habitat heterogeneity can be considerable, and some breeding birds do occupy poor-quality habitats (Ch. 5). The question is whether, for a given area, local crowding effects within and adjacent to prime breeding habitat (resulting from exclusion of sexually mature birds) is more or

less important than the possible regulatory effect of movement to poorer quality habitat. Ultimately, the answer to such questions for oystercatchers is likely to lie in understanding the long-term fitness trade-offs for an individual which chooses to join a long queue for a high-quality territory, as opposed to one which joins a short queue for a lower quality territory (Ens *et al.* 1995, Heg 1999, Bruinzeel & Pol 2004). Despite a paucity of data for the African Black Oystercatcher, exclusion of sexually mature birds from preferred breeding habitats is currently the best empirically supported mechanism of local population regulation.

The simplest way in which territorial exclusion can lead to population regulation is by birds with fixed, contiguous territories completely excluding other, sexually mature birds (Newton 1998). If the floater population increases, the *per capita* reproductive output of the entire population decreases and the population will stabilise when recruitment is balanced by mortality. Similarly, if floater numbers decrease, the average *per capita* reproductive output of the entire population will increase and so the entire population will once again increase to equilibrium. This simplistic example underpins the basic concept of regulation which can be defined as "...a negative feedback mechanism that increases demographic rates when population size declines (and *vice versa*) relative to some equilibrium...." (Rodenhouse *et al.* 1997). However, it also illustrates the important point that a negative feedback mechanism does not necessarily involve density dependence (Rodenhouse *et al.* 1997). The *per capita* reproductive output of the entire population does decrease with an increase in population size, but this is not due to a functional relationship between population density and reproductive output.

This simplistic mechanism of population regulation was incorporated into Population Viability Analyses (PVAs) for the African Black Oystercatcher (Ch. 6). The major shortcoming of these PVAs, however, is that they require breeding populations to be fixed at some upper limit, without any underlying mechanism as to how breeding densities (and ultimately total population sizes) are established. However, in the case of territorial animals, territory size may vary according to resource (e.g. food) abundance so that territorial individuals maximize the net benefits of maintaining a territory (Carpenter 1987a).

Similarly, conspecific pressure may influence territory size such that territories are not fixed for a given resource level, but are compressed (Vines 1979, Patterson 1980). If territories are compressed, more birds are able to establish breeding

territories than would otherwise be the case. Thus, territory size may depend on the proportion of the total population that can breed at any one time, even though a large fraction of mature birds are excluded (Krebs 1970). The latter form of density dependence has been demonstrated for Eurasian Oystercatchers where breeding populations increased in concert with an increase in the floater population (K.B. Briggs, K.-M. Exo unpubl. data, cited by Goss-Custard *et al.* 1996a).

Understanding how characteristics of the environment (e.g. food abundance), of behaviour (e.g. territoriality) and of populations (e.g. densities) interact is essential in understanding, for example, how populations respond to changes in habitat quality (Patterson 1980). The possible population consequences of habitat loss for European Oystercatchers have already been well studied, both at local and continental scales (e.g. Sutherland & Dolman 1994, Dolman & Sutherland 1995, Goss-Custard *et al.* 1996a, Durell *et al.* 1997), but little is known about how African Black Oystercatcher populations may respond to habitat loss or degradation, even at a local scale. Such insights, however, cannot be gained without some understanding of the way in which population and environmental variables are interlinked.

The aims of this study were therefore to:

1. Develop a simple model of oystercatcher population dynamics which can encapsulate the relative importance of a) resource levels/habitat quality, b) territorial behaviour, and c) population densities/demographic rates.

2. Use population data from four sites, spanning periods of stability and transience, to assess the validity of the model and to attempt to assess a) whether there is any density-dependent effect of the total *potential* breeding population on the *actual* breeding population and, b) the relative importance of habitat quality and conspecific pressure in determining breeding densities.

3. To assess the carrying capacity of local breeding populations, particularly with reference to the effect of the strength of the density-dependent relationship.

4. To assess the importance of density dependence (as outlined in 2. above) in the context of stochastic processes acting on local populations (in particular, variability in breeding success and mass mortalities).

METHODS

Definition and characterisation of local populations, and assumptions underlying the model

For this study, four local South African breeding populations were identified, two on islands off the west coast (Malgas Island (33°03′S, 17°56′E) and Jutten Island (33°05′S, 17°58′E)), and two at sites on the south coast mainland (Goukamma Nature Reserve (34°04′S, 22°50′E) and De Hoop Nature Reserve (34°29′S, 20°30′E))(Fig. 1.1). All four populations were considered to be closed, a reasonable assumption based on high levels of natal philopatry and site fidelity. These are known to be extremely high for both island populations (Ch. 5). They may not be as high for mainland populations (Ch. 5), but the spatial scales of the mainland studies, 13.5 km at De Hoop and 14.1 km at Goukamma make the assumption reasonable.

For immature birds, only the fledging success of breeding populations, and average yearly survival rates determined population sizes, while the size of the nonbreeding population of mature birds was determined by age-related survival rates and the degree of exclusion operating on the breeding grounds during the breeding season.

Furthermore, breeding populations outside of the breeding season were not considered as being spatially different from those during the breeding season; i.e. birds were treated as being territorial year-round. Thus, breeding populations were assumed to experience similar habitat/resource conditions throughout the year.

Although, there is little hard evidence to validate or invalidate many of these assumptions, much of the life-history information about African Black Oystercatchers suggests that the assumptions are reasonable. Compared to other species of oystercatchers (and primarily races of Eurasian Oystercatcher), the African Black Oystercatcher has an altogether less complex life-history in that adults are not migratory (Hockey 1996) and typically hold the same feeding territories year-round, although they do join high-tide communal roosts in the nonbreeding season (Hockey 1983a, Hockey 1985).

In migratory Eurasian Oystercatchers, density-dependent processes in the nonbreeding season, when birds are aggregated on foraging areas, may have a strong influence on population dynamics. In particular, increased interference-related competition for food among adults on wintering grounds appears to impact annual

mortality by reducing the fitness of early spring migrants (Durell *et al.* 2000). By contrast, density-dependent mortality among breeding adult African Black Oystercatchers is unlikely, because of their year-round territoriality (Hockey 1996).

Little is known of the biology of nonbreeding sexually mature oystercatchers, but density-dependent mortality, similar to that described in adult Eurasian Oystercatchers, may operate among immature African Black Oystercatchers. The reasons for inferring this are threefold. Juvenile and immature oystercatchers have complex movement patterns: many travel long distances (some >2000 km) to nursery grounds in Namibia and southern Angola that lie outside the species' breeding range, before returning 2-3 years later to their natal areas (Hockey *et al.* 2003, Rao 2005). Unlike adults, immatures frequently feed in flocks at high-quality feeding grounds and do not have spatially structured feeding territories (Leseberg 2001, Rao 2005). Consequently agonistic interactions among foraging juveniles/immatures could be predicted to be far higher than among territorial adults.

However, aggressive encounters and intra-specific kleptoparasitism appear to be relatively infrequent, certainly when compared with Eurasian Oystercatcher (Ens & Goss-Custard 1984, Sitters 2000, Leseberg 2001). There is no convincing evidence that aggressive encounters and intra-specific kleptoparasitism have a significant effect on intake rates, and mortality rates appear extremely low (Leseberg 2001). Therefore, although it is possible that density-dependent effects operate among foraging immatures, the model developed here investigates only the possible density-dependent effect of the potential breeding population on the realised breeding population.

Model structure and development

The model structure used in this study was virtually identical to that used for stochastic model simulations of single populations (Ch. 6), except that the breeding population could now be potentially influenced by the total number available to breed – hence introducing the possibility of density-dependence.

There are two critical components to the model: firstly, describing how the population is regulated by territorial exclusion of sexually mature adults; and secondly describing the influence of the total potential breeding population on the numbers that do breed (i.e. the possible density-dependent effect).

For the African Black Oystercatcher, population regulation by means of territorial exclusion is suspected, based on the evidence presented earlier. However, although the species' global population size has increased over the past 25+ years (Ch. 2), how exclusion of sexually mature birds may vary with population size has not been documented (because there are very few long-term count data of breeding numbers as distinct from total numbers). Many breeding populations of Eurasian Oystercatchers in Britain have remained fairly stable despite a large increase in the total population (Goss-Custard *et al.* 1995), suggesting little density-dependence, but strong territorial regulation of the population (through exclusion of sexually mature birds). Two other (and probably more reliable) sources of empirical data, both for Eurasian Oystercatcher, suggest that as a result of competition for territories, the proportion of adults that are nonbreeders increases with the total number of potential breeders (K.B. Briggs, K.-M. Exo unpubl. data, cited by Goss-Custard *et al.*1996a), even though the number of breeders also increases. This suggests that there is a density-dependent effect operating. Whether or not density-dependence is operating (in terms of the potential breeding population influencing the number that do breed), if the *proportion* of nonbreeders increases with an increase in the total number of potential breeders, then the possibility of population regulation arises because in the dynamic situation, the net *per capita* growth rate of the entire population will decrease as population size increases. Eventually, population size will stabilize when the floater population reaches a level where productivity is fully balanced by mortality. Because of the logarithmic nature of the relationship inherent in Fig. 7.1 (which is based on

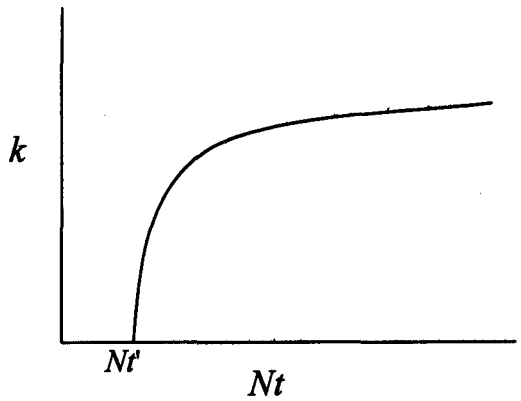

Fig. 7.1. An asymptotic function illustrating how the proportion of mature birds excluded varies with the number of potential breeders in the model. k = proportion excluded, Nt = total potential breeding population, and Nt' = potential breeding population size at which exclusion begins. Modified from Goss-Custard (1980).

observational data - K.B. Briggs,K.-M. Exo unpubl. data, cited by Goss-Custard *et al.*1996a), even over a relatively small range in population size, populations should reach stability fairly quickly because the regulatory effect (a decrease in the average *per capita* growth rate over time, with an increase in population size) is strong. Running time-dependent population models incorporating the highly asymmetric competitive relationship inherent in Fig. 7.1 (which describes how exclusion varies with population size) shows that even populations with high reproductive rates will reach equilibrium fairly quickly in the dynamic situation. (Goss Custard *et al.* 1996a).

Thus, based on observation, the simplest way in which the proportion of potential breeders excluded varies with an increase in the total potential breeding population can be described by a power function (see Fig. 7.1), i.e.

$$\Delta k \propto \Delta(\ln Nt) \quad \text{.....Eq.7.1,}$$

where k describes the proportion of the potential breeding population excluded and Nt describes the total potential breeding population. It is important to emphasize that the proportionality expressed in Eq. 7.1 makes no explicit statement regarding density dependence. It only reflects the way in which exclusion varies with population size and hence provides a powerful mechanism for population regulation in the dynamic situation. Eq. 7.1 can be expressed as an equality as follows:

$$\Delta k = b * \Delta(\ln Nt) \quad \text{.....Eq.7.2,}$$

where b is the constant of proportionality. Up to this point, the number excluded has been expressed as a proportion (i.e. k), but k can also be expressed as a 'k-value' similar to the way in which Varley and Gradwell (1960) defined mortality in key-factor analysis (Goss-Custard 1980), i.e.

$$k = \ln Nt - \ln Nb \quad \text{.....Eq. 7.3,}$$

where Nb is the number of birds that breed. Note that however k is expressed, the linearity of Eq. 7.2 still holds, but expressing k as in Eq. 7.3, allows for density

dependence to be modeled on a convenient scale between zero and 1 (Goss-Custard 1980). Rearranging Eq. 7.2 gives:

$$b = \frac{\Delta k}{\Delta(\ln Nt)} \quad \text{.....Eq. 7.4.}$$

Substituting the value of k (Eq. 7.3) gives:

$$b = \frac{\Delta(\ln Nt - \ln Nb)}{\Delta(\ln Nt)} \quad \text{.....Eq. 7.5.}$$

From Eq. 7.5 it is clear that if the total potential breeding population has no influence on the breeding population, then Nb remains constant and Eq. 7.5 thus becomes:

$$b = \frac{\Delta(\ln Nt)}{\Delta(\ln Nt)} = 1 \quad \text{.....Eq. 7.6.}$$

However, if every potential breeder becomes a breeder, then the influence of the potential breeding population on the breeding population can be thought of as infinite or undefined. In this case Nt must equal Nb and hence Eq. 7.5 becomes:

$$b = \frac{0}{\Delta(\ln Nt)} = 0 \quad \text{.....Eq. 7.7.}$$

Any intermediate value of b will result in the total potential breeding population having some influence on the breeding population through conspecific pressure, but unless b=0, the proportion of birds excluded will *always* reach an asymptotic phase, due to the logarithmic relationship inherent in Eq. 7.1. The asymptotic nature of the relationship when numbers of competitors are relatively high means that the proportion of competitors excluded (k) as the total number of competitors (Nt) increases very nearly approximates a constant, even when there is very large variation in Nt. Note that natural log values have been used here, but the same conclusions hold provided that both the change in k and the change in Nt are expressed with the same logarithms. b-values have been used extensively to describe density-dependence

effects in oystercatcher population dynamics, not only in the context of potential breeders influencing breeding numbers, but also to describe the possible influence of conspecific pressure on densities of migratory Eurasian Oystercatchers on the nonbreeding grounds (Goss-Custard *et al.* 1996a, 1996b).

However, a slightly different conceptualization of the *b*-value is advanced here (cf. Goss-Custard 1980, Goss-Custard *et al.* 1996a, 1996b). This stems from the need to distinguish between density dependence and population regulation. The two concepts are frequently confused, possibly because traditional studies of density-dependent effects (e.g. the influence of population density on aspects of breeding success) have focused on processes that *also* act in a regulatory fashion – i.e. density-dependent effects which also involve a negative feedback process. However, this is not necessarily the case (Rodenhouse *et al.* 1997). Because birds compete for territories, the density-dependent effect can be viewed as the possible influence of the potential breeding population on the breeding population.

In this context, conspecific pressure influencing breeding population density therefore provides a perfect example of a situation where the density-dependent effect acts *directly contrary* to the regulatory process, but the population can nonetheless be regulated over time purely by territorial exclusion, because the nature of territoriality itself (i.e. a highly asymmetric form of competition) is such that birds prevented from breeding will accumulate at a much faster rate than the number of breeders, even if the breeding population increases rapidly (i.e. $b << 1$).

At this stage, the model only describes a change in the degree of exclusion (k) with a change in the population size of potential breeders (Nt) (see Eq. 7.2). However integrating the differential form of Eq. 7.2, i.e.:

$$\int dk = b * \int d(\ln Nt) \quad \text{.....Eq. 7.8,}$$

gives:

$$k = b * \ln Nt + C \quad \text{.....Eq. 7.9.}$$

Note that Eq. 7.9 reflects the equation for a straight line of the form y = bx + c. Therefore C in Eq. 7.9 reflects the x-intercept and making $k = 0$ solves for C. Thus Eq. 7.9 becomes:

$$k = b * \ln Nt - b * \ln Nt' \quad \text{.....Eq. 7.10,}$$

where Nt' reflects the population size at which exclusion begins. Substituting for k in Eq. 7.3 and rearranging gives:

$$\ln Nb = \ln Nt - b * \ln Nt + b * \ln Nt' \quad \text{.....Eq. 7.11.}$$

Thus the degree of exclusion (k) (and hence the breeding population size) is dependent on the potential breeding population size at which exclusion begins (Nt'), the total potential breeding population (Nt) and b. These aspects are incorporated into Fig. 7.2.

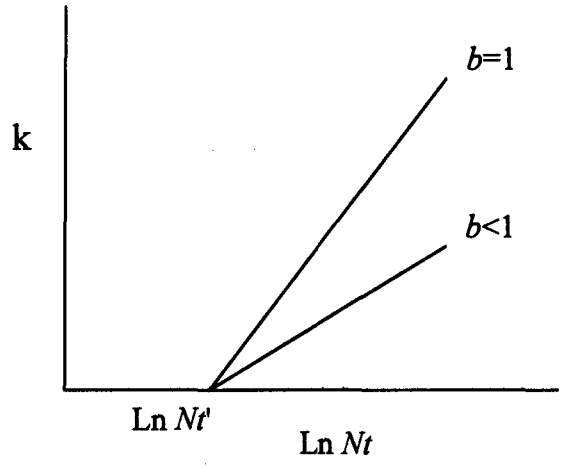

Fig. 7.2. Graphical representation of the way in which density dependence can be modeled. Where b =1, the number of birds breeding does not depend on the total number available to breed. However, when b<1, then the number breeding depends both on Nt' and on the slope, b. Modified from Goss-Custard (1980). (Refer also to Eq. 7.9 and Eq. 7.10).

There are a few important points to make regarding the explanatory power of and the assumptions inherent in the model as presented here. Firstly, b is a constant reflecting

an *evolved system of competitive asymmetry*, and hence is both independent of population size (as reflected in Eq. 7.8), and of habitat quality. The validity of this assumption for the African Black Oystercatcher is discussed later; however, it is important to point out that this does not mean the model ignores aspects of habitat quality (e.g. food availability) as an important factor influencing territorial aggression (and hence exclusion). Rather (from Eq. 7.10), Nt' reflects the 'contribution' of aspects of habitat to overall territorial aggression (and hence exclusion) and this (rather than b) varies with variation in habitat quality. The term $b*\ln Nt'$ is therefore descriptive of the territoriality of the animal in a particular environment. Thus, besides changing basic demographic rates, the effects of changes in habitat quality on territoriality can also be modeled by varying Nt', the underlying assumption being that improved habitat (e.g. increased food availability) should result in an increase in Nt' because the average optimal territory size will decrease (i.e. more birds can settle before exclusion occurs). This idea is illustrated graphically in Fig. 7.3.

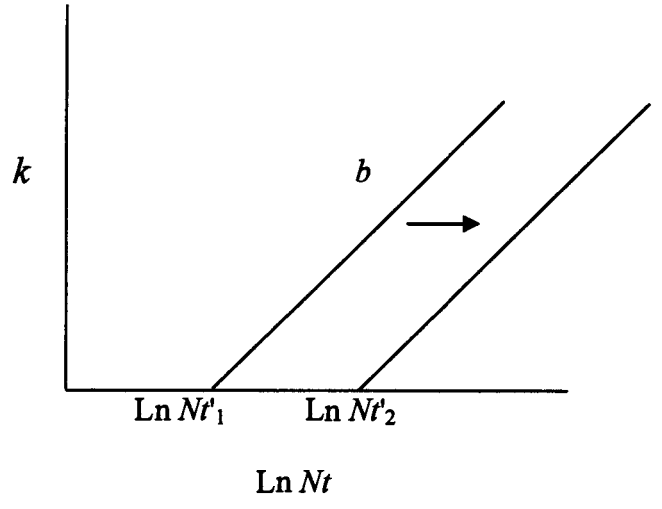

Fig. 7.3. Diagram illustrating the way in which improvement in habitat quality was modeled. The change in habitat quality is hypothesized to lead to a reduction in optimal territory size and is reflected by an increase in Nt' in the model, with b remaining constant.

The increase in aggression with an increase in population density (and hence the increase in the proportion of sexually mature birds excluded) is described by the term

b*lnNt in the model. Thus, the degree of exclusion, k (and hence breeding numbers and total population size) is dependent on both Nt' and Nt, as well as b.

The model further assumes that prey depletion does not play an important regulatory role in African Black Oystercatcher population dynamics. This appears to be a reasonable assumption. On rocky shores, the most important prey items for oystercatchers are mussels (primarily *Perna perna* and *Mytilus galloprovincialis*, depending on the region) and limpets (primarily *Scutellastra granularis*). While oystercatchers may heavily impact limpet densities (Hockey & Branch 1984), they typically switch to mussels as a primary food source in the case of local limpet depletion (Ch. 2). The relatively fast-growing mussel species typically occur at high densities, are abundant in the intertidal and are regulated by self-thinning rather than by predation (Griffiths & Hockey 1987).

On sandy shores, the major food source for oystercatchers is the white mussel *Donax serra* and oystercatchers have a negligible impact on the abundance of this species (Ward 1990). Thus Nt' is assumed to be independent of the local population density.

This is an important assumption, because if oystercatchers strongly influence overall prey abundance then, as the number of competitors increases, indirect competition for prey (exploitative competition) as well as direct competition for space (interference competition) may limit local population size. In the context of the model presented here, only the latter form of competition (i.e. territoriality) is considered, whereby increasing proportions of sexually mature birds are excluded from preferred breeding habitats as population size increases.

Although the model does not consider the possible regulatory function of any form of density-dependent mortality, at least one study of Eurasian Oystercatcher incorporating both empirical evidence and game theoretic models of oystercatcher foraging behaviour indicated that over a range of population sizes density-dependent starvation occurred as a result of interference competition without prey depletion having a significant influence (Goss-Custard *et al.* 2001). This further supports the contention that exploitation competition and its possible impacts (e.g. reducing adult survival and/or breeding success) is highly unlikely to influence oystercatcher population dynamics.

The density-dependent effect described above was incorporated into the population model as a discrete process. Thus, the attempts potential breeders to

establish territories on the breeding grounds were assumed to occur synchronously and instantaneously, at the beginning of each breeding season.

The degree of synchrony with which potential breeders attempt to establish territories may influence the number of birds which successfully establish territories (Maynard Smith 1982). Little is known regarding this possible effect for African Black Oystercatchers, and synchrony in the attempts to establish territories is therefore assumed for the sake of simplicity.

Model calibration and application

Estimating parameter *b* is difficult in practice because, for a given area, both the total number of potential breeders as well as the number of breeders needs to be known. Furthermore, a situation where the population is changing over time is required and the change in population numbers has to be large in order to achieve reasonable estimates (Goss-Custard *et al.* 1996a). Under non-equilibrium conditions, *b* will vary unpredictably over a small population range, due to inertial effects. For example, there may be a lag phase between the time at which individuals attempt to establish territories and when they do obtain breeding territories. It may also be difficult to estimate the number of potential breeders in a given area. As a result, even for Eurasian Oystercatcher - one of the best-studied shorebirds in the world - there are only two studies where the density-dependent effect of the potential breeding population on the realized breeding population has been estimated (K.B. Briggs, K.-M. Exo unpubl. data, cited by Goss-Custard *et al.* 1996a). These studies yielded a different value for *b* at the two sites, suggesting that the density-dependent effect may also be site dependent. However, this study of African Black Oystercatchers assumes a constant *b*-value across sites (as well as over a large range of population densities).

For African Black Oystercatchers, there is only one study site where both the total potential breeding population and the breeding population have been quantified (and where the population has changed over time), namely at Goukamma Nature Reserve. However, the change in population numbers at this site has been small and there is likely to be inaccuracy in the measure of the potential breeding population due to the difficulties of estimating the total size of the non-breeding fraction. To attempt to estimate *b* for African Black Oystercatchers, a different approach was therefore taken using only estimates of the breeding population over time at the four study sites.

Count data

Population trajectories for the four sites are illustrated in Fig. 7.4. All counts at all sites were undertaken during the breeding season. For all sites, all yearly estimates represent an average of between two and four summer counts except for count data from 1976 and 1980, which represent only single counts undertaken in early January. In estimating average breeding population sizes, counts were restricted to the mid to late period of the breeding season (between January and early March), to minimize possible inclusion of non-territorial birds, particularly at the three sites where uncertainty exists in estimates of the number of breeding pairs (i.e. De Hoop N.R., Malgas Island and Jutten Island). This rationale is based on the hypothesis that most competition for territories takes place at the beginning of the breeding season. While there is little evidence to substantiate this assumption for African Black Oystercatchers, detailed observations of Eurasian Oystercatchers show that fierce competition for breeding space takes place mostly in early spring (Heg 1999). The data incorporated in this study thus represent a range in terms of the certainty with which the actual breeding population is being estimated (as opposed to erroneous inclusion of adult, non-territorial birds).

The most accurate data come from Goukamma Nature Reserve. At this site, nests and chicks were monitored in every year during which counts were made (except for 1980). Count data represent the average number of birds either attempting to breed (making nest scrapes) or breeding (known to have incubated eggs and/or hatched chicks). Furthermore, oystercatcher densities at Goukamma are low, making it easy to identify pairs and associate them with relevant evidence of breeding activity (even for pairs with disjunct breeding and feeding territories). Count data for De Hoop Nature Reserve represent only an estimate of the average number of pairs, based simply on observation of spatial association between individual birds. However, because densities at De Hoop are also reasonably low (currently *ca* 5 birds.km^{-1}) and birds are distributed linearly along the coast, it is likely that this estimate of breeding pairs is fairly accurate. Furthermore, repeat counts in the same season are very similar (less than 3% divergent), suggesting that estimates do indeed represent resident territorial birds. At De Hoop Nature Reserve, small groups of between three and eight apparently non-breeding birds interspersed between territorial pairs were also regularly identified over the years, during the mid to late summer months. At both sites larger groups (15–62 individuals) of nonbreeding birds adjacent to breeding

areas have been observed over the same period (A. Scott unpubl. data, Oystercatcher Conservation Programme unpubl.data., Cape Nature Conservation unpubl. data.). Many of these individuals are likely to be sexually mature birds which have returned to their natal grounds, but this proportion cannot be reliably estimated, because (a) there is no reliable way of distinguishing sexually mature birds (>3-4 years of age) from immature birds (2-3 years of age), and (b) it is not certain whether all or a fraction of the birds in these groups were originally reared by breeding birds in the study areas.

The greatest uncertainty regarding estimation of the breeding population attends data from Jutten and Malgas Islands. These islands support very high densities of oystercatchers: on Jutten and Malgas Island, densities of resident birds are approximately 69 birds.km^{-1} and 73 birds.km^{-1} of shoreline respectively, making estimates of the number of territorial breeding pairs based simply on spatial association almost impossible. However, attempts at counting pairs during the breeding season based on spatial associations were made in the early 1980s and in all years from 1998 (P.A.R. Hockey unpubl. data, D.Loewenthal unpubl. data.). For all the latter counts, sexes were distinguished on bill morphology (Hockey 1981, Hockey & Underhill 1984), increasing the probability that closely associated individuals of opposite sexes were breeding pairs. Based on these data, the proportion of birds on Malgas and Jutten Island that are breeding pairs at the height of the breeding season (January) is greater than 90% and count data for the two islands were therefore assumed to represent the breeding population. Most of the mature nonbreeding birds reared on islands appear to spend most of their time on the adjacent mainland coast (<1.5 km away, but very poor quality breeding habitat) from which they make forays to the islands (Ch. 5): Oystercatcher densities on these mainland shores in the mid to late breeding season are extremely high, averaging 10-15 birds.km^{-1} (based on five years of count data between 1997 and 2002). This is nearly four times the average density on rocky shores on the west coast (Ch. 2), suggesting that a large proportion of these are birds excluded from the islands by territorial pairs. Stretches of mainland coastline progressively further from, but still within *ca* 10km of these two islands, and representing all three shoreline types (as defined in Ch.2), also support densities well above the overall average for each of these habitats on the west coast (Oystercatcher Conservation Programme, unpubl. data).

Further evidence to support the assumption that summer count data accurately represent the breeding populations on Malgas and Jutten Islands comes from a study over two years (1998/1999 and 1999/2000) when the islands were exhaustively searched for nests over a period of between four and six days between December 11 and December 21. At this stage of the breeding season, the majority of breeding birds are at the incubation phase of their breeding cycle on the Saldanha Bay Islands, the peak egg-laying period being between mid-December and mid-January (Hockey 1983b). The main reason for this exercise was to find nests with incubating birds, so that pairs could be retrapped using walk-in traps (Ch. 5): fresh nest scrapes as well as pairs with chicks were also recorded. Pairs with chicks were identified based on the behaviour of adult birds (Baker & Hockey 1984). The number of individuals estimated to be breeding or attempting to breed were as follows (corresponding mean counts of individuals from the same season in parentheses): Malgas - between 110 (92*) and 124 (157) individuals for December 1998 and December 1999 respectively; Jutten 168 (197) and 192 (228) birds. Given that some breeding pairs would not have started breeding and some might not have re-initiated breeding activity following egg loss, there appears to be fairly good agreement between estimates of number of breeding pairs and adult counts – at least in these years. (* the count of 92 birds at Malgas in 1998/1999 is almost certainly an underestimate because access to parts of the island was compromised by breeding colonies of Cape Cormorants *Phalacrocorax capensis*).

At all four sites, populations have increased since the late 1970s/early 1980s, but these increases have not been steady over the last 25+ years. Rather, at all four sites, numbers appear to have remained stable up to the late 1980s/early 1990s, then increased relatively rapidly (particularly at De Hoop and Goukamma Nature Reserves) and then rapidly stabilized again (Fig. 7.4, Results). At Malgas and Jutten Islands, this pattern is less convincing, due to larger year-to-year fluctuations in numbers. Despite fluctuations, at both islands, the lowest counts since 1995 have been higher than the highest counts pre-1995. Statistical analysis of the count data confirms this conclusion (Table 7.1, Results). Whatever the pattern of increasing numbers, there are two main reasons which have been hypothesized as the cause of population increases at these sites – improved protection status and/or increased food availability (Ch. 2). De Hoop Nature Reserve was initially proclaimed in 1957. However, prior to 1986, when the area was declared a Marine Reserve, angling, bait-collecting and off-

road vehicles were all permitted along the coastline. Goukamma Nature Reserve was proclaimed in 1960, but the area was only designated a Marine Reserve in 1990. At this time, all bait-collecting was stopped, along with the use of off-road vehicles associated with commercial oyster harvesting, and patrols were initiated to prevent illegal night-time shore angling (Leseberg *et al.* 2000). At Jutten and Malgas Islands there was a dramatic increase in the proportion of the alien invasive Mediterranean Mussels *Mytilus galloprovincialis* in the oystercatchers' diet between the early 1980s and the early 1990s (Hockey & van Erkom Schurink 1992), with no apparent trend subsequent to this (Fig. 2.1): this novel food source has certainly increased food availability for oystercatchers on these islands (Ch. 2). The protection status of the islands was also significantly improved in 1985, when they were incorporated into the West Coast National Park. Prior to this there was much seasonal human disturbance on Malgas Island due to guano collecting activities (Crawford *et al.* 1995). If, as hypothesized, protection and improved food supply have benefited oystercatchers, then there is a clear lag phase between the time at which conditions improved and the time at which breeding populations increased (Fig.7.4). Using the simple model presented here to try to explain the patterns in population numbers at the four localities and assess the strength of density dependence (*b*-value), an attempt was also made to put forward a reason for this lag-phase.

Model calibration

Statistical analysis of count data for breeding populations at all four sites indicated that populations were stable up until the late 1980s/early 1990s and again (but at a higher level), since the early to mid-1990s (Table 7.1, Results). This pattern of population changes at the four sites formed the basis of model manipulations and the estimation of *b*.

For all simulations, mean post-fledging, immature and adult survival rates were kept constant, and were the same as those incorporated into the population model developed in Chapter 5. Data on average breeding success (fledglings.pair^{-1}.year^{-1}) for each local breeding population were obtained from the following sources:

De Hoop Nature Reserve: Breeding success of 15-20 breeding pairs was documented over six years between 1984 and 1990 (A. Scott unpubl. data.). These data cover two years before the area was declared a Marine Reserve, and four years subsequently.

There was no significant difference in fledgling success pre- and post-Marine Reserve proclamation (A. Scott unpubl. data.) and the mean fledging success was 0.77 fledglings.pair^{-1}.year^{-1}).

Goukamma Nature Reserve: All breeding pairs and their performance were monitored between 1990 and 2004, after the Marine Reserve was proclaimed. Between nine and 17 breeding pairs were studied annually over this 14-year period. There was no significant trend in breeding success over this period (see Fig. 7.5, Results) and the average success was 0.41 fledglings. pair^{-1}. year^{-1}.

Malgas and Jutten Islands: No detailed nest monitoring data exist for these two islands. Breeding success was assumed to be 0.91 fledglings.pair^{-1}.year^{-1}, based on monitoring of between 48 and 69 pairs per year over four years at nearby Dassen Island (33°26'S, 18° 05'E).

Based on the hypotheses that either breeding success has improved (modeled as an increase in the average number of fledglings.pair^{-1}.year^{-1}) and/or the average optimal territory size of breeding birds has decreased (modeled as an increase in Nt') following protection and/or improved food supply, both of these parameters were manipulated in the model for a given b-value, and compared with the observed data. (Recall that in the context of the model, b is considered to be independent of habitat quality).

To attempt to simulate the observed patterns of periods of population stability and population change in the context of the model, the basic procedure was as follows:

(1) To observe the possible effect of a change in Nt' on breeding population numbers, b, as well as the average breeding success were kept constant. A value for Nt' was then selected to give the correct mean breeding population size (see Table 7.1, Results) before the late 1980s/early 1990s (the time at which populations appear to have increased in response to improved conditions). Nt' was then increased by varying amounts at the time at which protection and/or food supply improved and the effect of this on breeding numbers was compared with the observed data. The procedure was repeated for various values of b.

(2) Although data from De Hoop N.R. and Goukamma N.R. appear to indicate no significant increase in breeding success following protection, this may simply be due to large inter-annual variability in breeding success (Fig. 7.5, Results). At Malgas and Jutten Islands, breeding success did appear to improve in the 1980s, as the proportion of *Mytilus* in the hard-shelled diet of adult oystercatchers increased (Hockey & van Erkom Schurink 1992, Fig. 2.1). Therefore, to investigate the possible effect of improved breeding success on breeding populations, a variety of much lower values for breeding success were arbitrarily chosen, for a given value of b. For each of these breeding success values, a value of Nt' was obtained to give the mean breeding population size between the late 1970s and early 1990s (see Table 7.1). The same procedure was followed as in (1) above, except that Nt' was held constant and breeding success was increased by varying amounts (up to and beyond the current mean values given). The effects of these manipulations on modeled population changes were then compared against observed data.

Estimating upper limits to local breeding populations

Because of uncertainty in the estimation of b, model projections were made for populations at each of the four localities, for a number of possible values for b, and the resultant upper limits to breeding numbers assessed. All projections assumed current mean breeding success and mean survival rates for post-fledging, immature and adult oystercatchers as used in Ch. 6. Projections were based on extending the duration of the simulations that were used to calibrate the model.

The effect of density dependence in the context of stochastic processes

Again, due to uncertainty in the estimation of b, stochastic simulations were undertaken using a variety of b-values. For each b-value, initial conditions were established based on current estimated mean breeding success. Current breeding populations were assumed to be stable (as seems to be the case). Thus, for each b-value, a site-specific Nt' value was chosen to give the correct observed current mean breeding population size (see Table 7.1, Results).

The most important stochastic processes which impact on African Black Oystercatcher populations are annual variability in breeding success and, for island populations, mass mortalities of breeding adults (Ch. 6). Annual variability in breeding success was therefore incorporated into models of population dynamics for

all populations (breeding success data (fledglings.pair^{-1}.year^{-1}) were pooled for pairs at each locality, giving an average value for each year), while additional mass mortalities were simulated only for populations on Malgas and Jutten Islands.

In terms of breeding success, there were six years of data for De Hoop N.R. (A. Scott unpubl. data) and 14 years of data for Goukamma N.R.. For Malgas and Jutten Islands, which lack current breeding success data, the data from Dassen Island were again used as a substitute. These data sets are smaller than those used in stochastic model simulations in Ch. 6. Normality was assumed, and normal distributions fitted to these data, based on the fact that the more extensive breeding success data for mainland populations were normally distributed (Ch. 6). Probabilities were applied to categories for fledging success ranked cumulatively in intervals of 0.09 fledglings.pair^{-1}.year^{-1}. The mid-point of each of these intervals was used as the value for each category. The resultant normally distributed, categorical data sets on fledging success probability provided the underlying variability for stochastic simulations.

Based on the severity and frequency of the two mass mortalities on the Saldanha Bay Islands (Ch. 6), mass mortalities were modeled as events with a 1-in-10 year probability and reducing adult survival from 96% to between 50% and 70%. The probability of a particular severity was modeled as a flat distribution – thus a mass mortality event was equally likely to reduce survival to 50% as opposed to 70%, or any other value between these extremes. (It is important to note that whatever the *b*-value, if the potential breeding population fell below Nt', then there could be no exclusion of sexually mature birds. In stochastic simulation models, therefore, b=0 when potential breeding populations fell below Nt').

For each locality, and for each *b*-value, 1000 200-year-runs were performed in a similar way to that done for stochastic model simulations in Ch. 6. Thus, outcomes of stochastic simulations were treated as sample populations amenable to statistical comparison.

Within-site population outcomes were compared using one-way ANOVAs with the strength of density dependence being the main effect. These analyses were followed by Tukey's HSD post-hoc tests.

RESULTS

Analysis of putative breeding population trends suggest that, although populations at the four study localities have increased over the last 25+ years (Fig. 2.3), most of this increase can be attributed to a short period between the early and mid-1990s.

Table 7.1. Analysis of trends in breeding population numbers at Goukamma Nature Reserve (GK), De Hoop Nature Reserve (DH), Malgas Island (MG) and Jutten Island (JU).

	Period	n	Av. No.	r	p	Period	n	Av. No.	r	p
GK	1980-1992	5	15	0.63	>0.1	1994-2005	12	34	0.39	>0.1
DH	1980-1991	8	46	0.51	>0.1	1994-2005	12	72	0.43	>0.1
MG	1976-1992	17	56	0.43	>0.25	1995-2005	11	127	0.11	>0.25
JU	1976-1992	17	133	0.02	>0.25	1996-2005	10	232	0.36	>0.25

At all localities, populations remained approximately stable between the late 1970s/early 1980s and early 1990s, and, at higher levels, between the mid 1990s and 2005 (Fig. 7.4, Table 7.1). This provided the basis for the calibration of the model. Breeding success data from De Hoop N.R. suggest that there was no difference in breeding success pre- and post-protection. Statistical analysis of these data confirm this (A. Scott unpubl. data). At Goukamma N.R., breeding success data only exist for the years after protection was implemented. However, there appears to be no trend of increasing breeding success in the years following protection. It could be argued that breeding success increased at first and then decreased due to density-dependent effects. However, visual inspection of the data does not support this hypothesis (Fig. 7.5).

Model calibration

Manipulation of fledging success, keeping Nt' constant: At De Hoop Nature Reserve and Goukamma Nature Reserve, the time between improved protection status and increases in breeding population numbers appears to be 3-5 years (Fig.7.4), while at Jutten Island and Malgas Island, this lag is approximately 7 years. At all sites, increasing breeding success at the time when protection improved resulted in

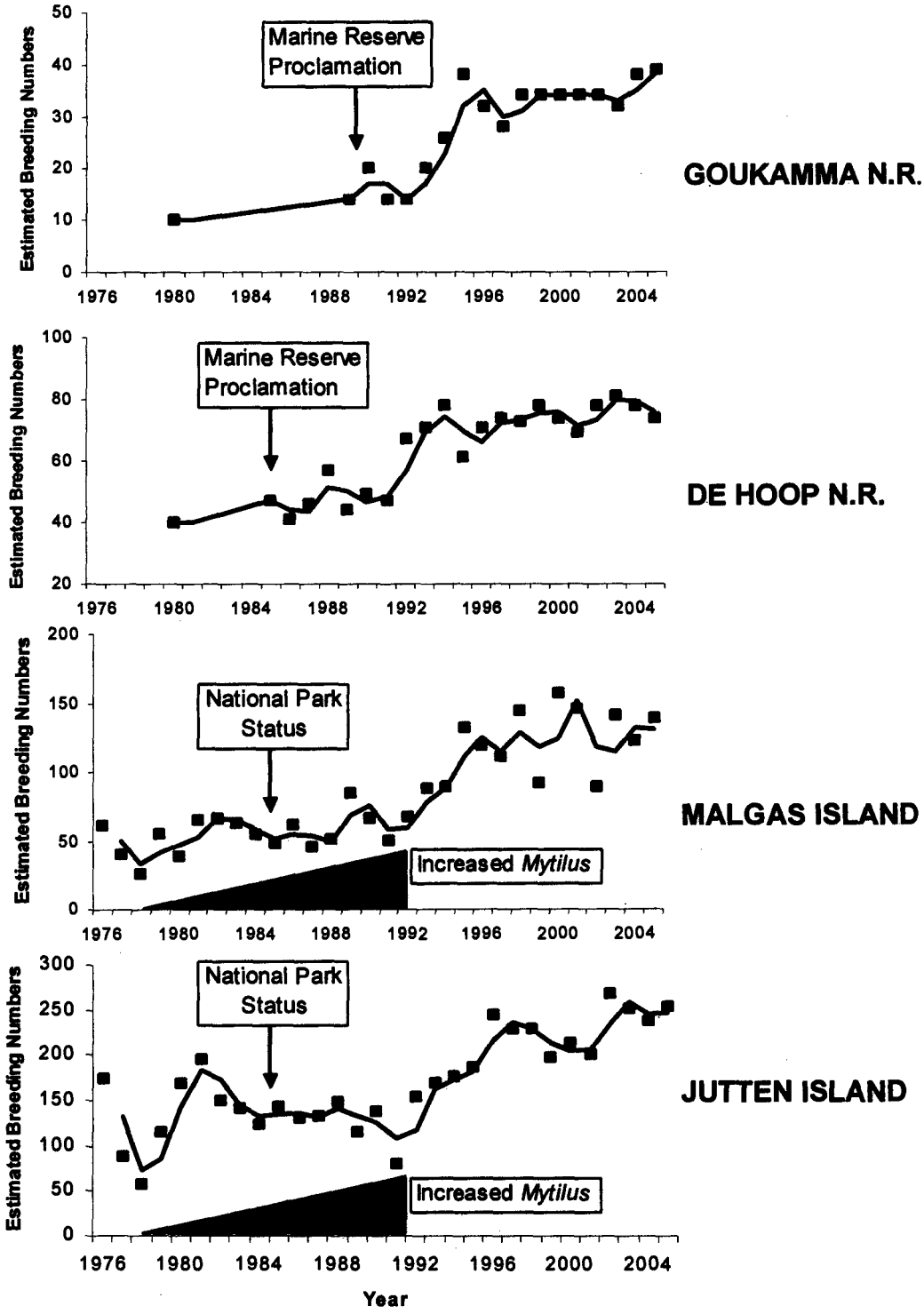

Fig. 7.4. Changes in estimated breeding numbers at four localities around the coast of South Africa together with hypothesized reasons for these trends, namely an increase in protection and/or an increase in the proportion of the Mediterranean Mussel *Mytilus galloprovincialis* in the hard-shelled diet of oystercatchers. Trend lines show 2-year moving averages.

breeding population increases which seemed to compare well with the lag phase between improvements in habitat quality and observed breeding population increases.

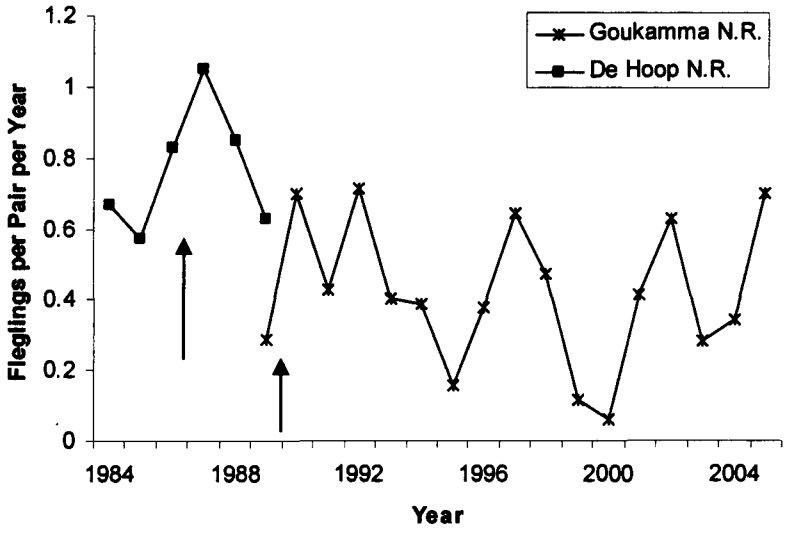

Fig. 7.5. Changes in the mean annual breeding success of African Black Oystercatchers at two sites on the south coast of South Africa. Arrows indicate the years in which protection was implemented.

However, improved breeding success could not explain the rapid population increases followed by stability that have occurred at the four sites. Even when mean fledging success was increased to more than double current estimates (a highly unlikely scenario), predicted rates of increase in the breeding population were much slower than those observed. This was true even for very low values of *b*, simulating high pressure for breeding space from floaters.

Using small *b*-values to attempt to calibrate the model eventually resulted in stable breeding populations that were far higher than observed stable breeding numbers. For example, trying to simulate breeding population changes at De Hoop N.R. by doubling the current breeding success and using very low *b*-values, resulted in breeding populations stabilizing at approximately 150 individuals (after approximately 50 years), compared to the current mean of 72 birds (Fig. 7.6). In order to achieve stable breeding numbers approximating the current observed average, a much weaker density-dependent effect (i.e. higher *b*-value) was required. This resulted in much slower increases in the breeding population and a much longer

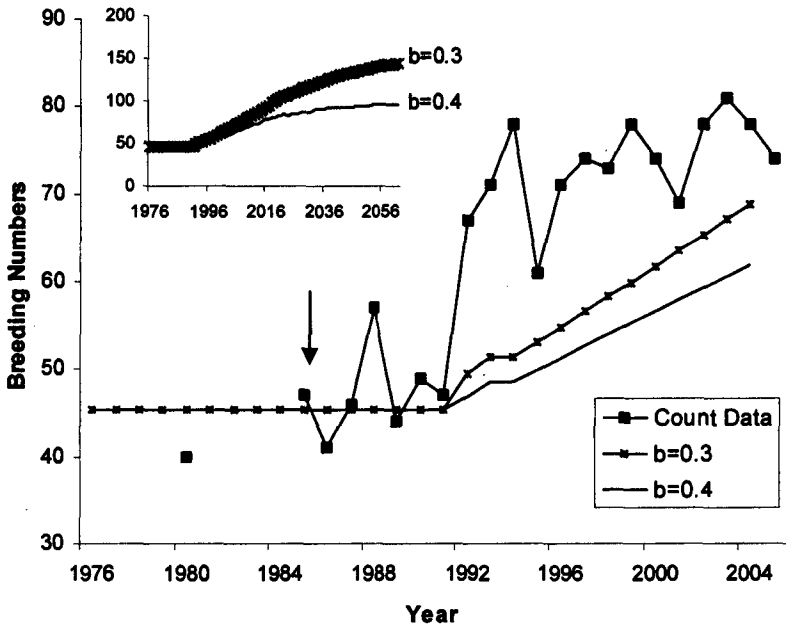

Fig. 7.6. Graphical illustration of the results of model simulations compared against count data from De Hoop Nature Reserve. The arrow marks the year in which breeding success was doubled from 0.77 to 1.54 fledglings.pair^{-1}.year^{-1}. Inset illustrates the time over which populations stabilize, for the given simulations shown in the main figure. *b*-values in these examples are small, simulating a strong density-dependent effect.

period to stability than that observed. Only one example is illustrated here (Fig. 7.6), but results from all other sites were similar.

Manipulation of Nt', keeping fledging success constant: At low values of *b*, manipulation of *Nt'* immediately following either improvement in food availability or increased protection resulted in initial, rapid increases in the breeding population. This was the case for all simulations and shows that, even at Goukamma N.R., where average breeding success is low, the initial size of the floater population was large enough to account for the increase in the breeding population as a result of changing *Nt'*. However, a secondary effect of increasing *Nt'* was a continued increase in the breeding population, although at a much slower rate, with the population eventually stabilizing. This pattern was similar for all sites, except that for low values of *b* this continued increase in the simulated breeding population was much more rapid for Jutten and Malgas Islands than for either De Hoop or Goukamma N.R. (Figs. 7.7-

7.10). For all sites, simulated increases were out of phase with real increases by between four to six years. However, if it is accepted that there is a real lag phase, and this is taken into account in the model, then for all sites the simulated pattern of population dynamics corresponds well with the data, but *only* if relatively high *b*-values are used. *b*-values higher than 0.8 resulted in secondary increases being negligible for all sites - at least over the period for which observational data exist. Figs.7.7-7.10 illustrate the point that as *b* is increased from 0.4 to 0.8, simulated breeding populations appear to fit increasingly more accurately the observed pattern of rapid increases in breeding numbers followed by stability.

However, model simulations for breeding populations at De Hoop and Goukamma also showed that populations became insensitive to any further increases in *b*, at a lower value of *b* (approx. 0.6) than was the case at Malgas and Jutten Islands, where the corresponding value of *b* was approximately 0.8 (Figs. 7.7-7.10).

Based simply on visual comparison of the model results and that of observational data from De Hoop and Goukamma, it is therefore possible to make an estimate for *b* of between approximately 0.6 and 1 (Figs. 7.7, 7.8). However, model simulations of island-breeding populations suggest that *b* is even higher and possibly in the region of 0.8 or greater (Figs. 7.9, 7.10) and it would certainly be reasonable to assign a value of between 0.6 and 1. The estimation of *b* thus depends essentially on minimising a model-generated, secondary increase in breeding numbers, in keeping with observed data (because observational data indicate that breeding numbers remained stable over the same period).

Differences between sites in terms of the sensitivity of the breeding population to changes in *b* (and especially at low values of *b*) can be explained by differences in reproductive rates. In the case of island populations, where average yearly fledging success is high, changing Nt' (i.e. allowing non-breeders to establish territories without resistance from breeders already holding territories) dramatically increases the population's reproductive output. This in turn leads to a much more rapid increase in the number of floaters, relative to sites where populations have a low reproductive output.

When *b* is small, differences in the reproductive output of populations between sites will give rise to relatively large differences in breeding population changes between sites. This can be attributed to the fact that an increase in the total potential

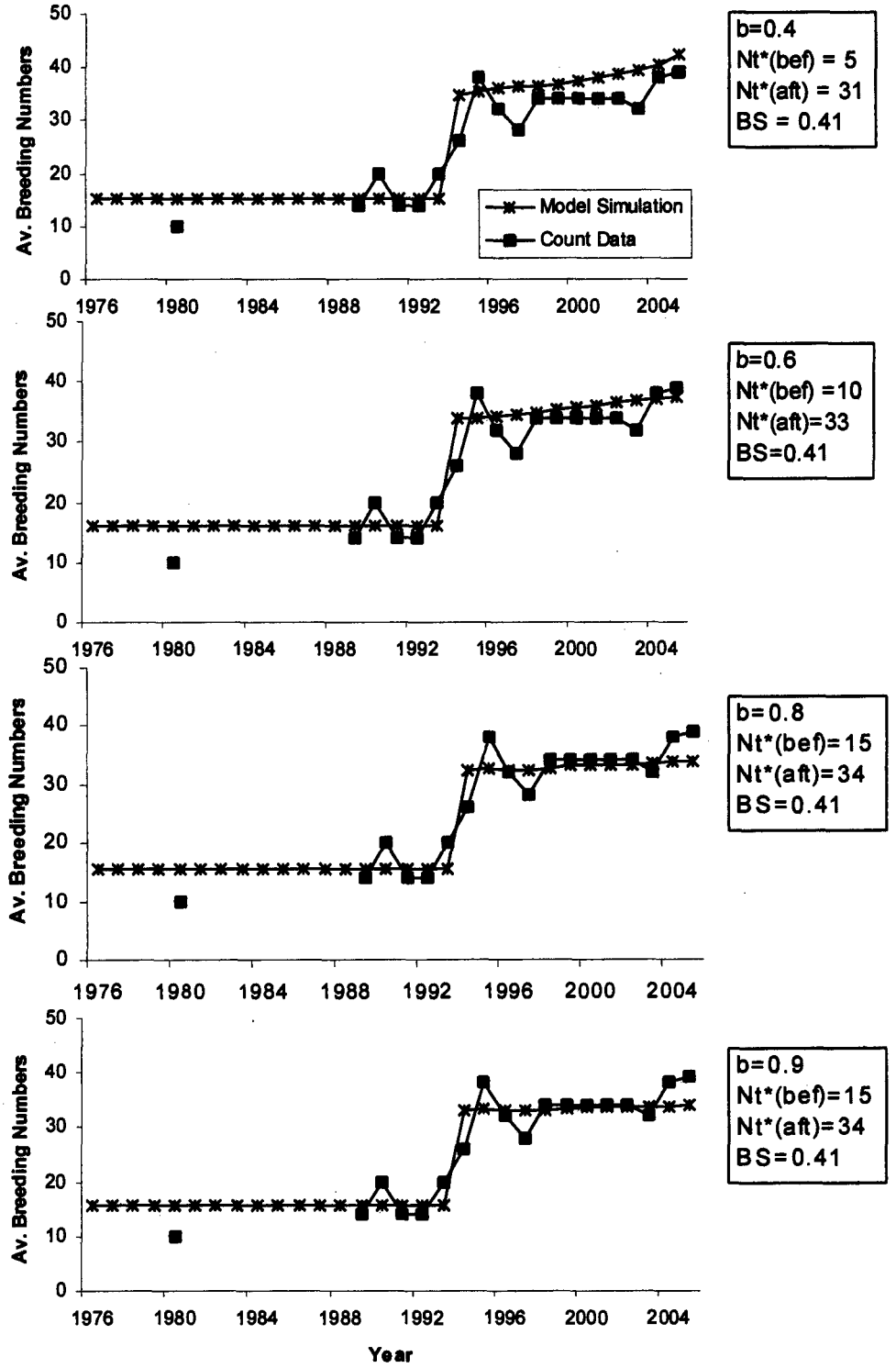

Fig. 7.7. Results of simulations used to attempt to estimate the density-dependent function, *b*, using count data from Goukamma N.R. BS = average breeding success (fledglings.pair^{-1}.year^{-1}), Nt^{*}(bef) = the value of Nt^{*} needed to fit the model to average breeding numbers before protection, Nt^{*}(aft) = the new value of Nt^{*}, used to fit the model to the average stable breeding population size after it increased and *b* = the strength of the density-dependent function used (low *b*-value reflects strong density dependence and *vice-versa*).

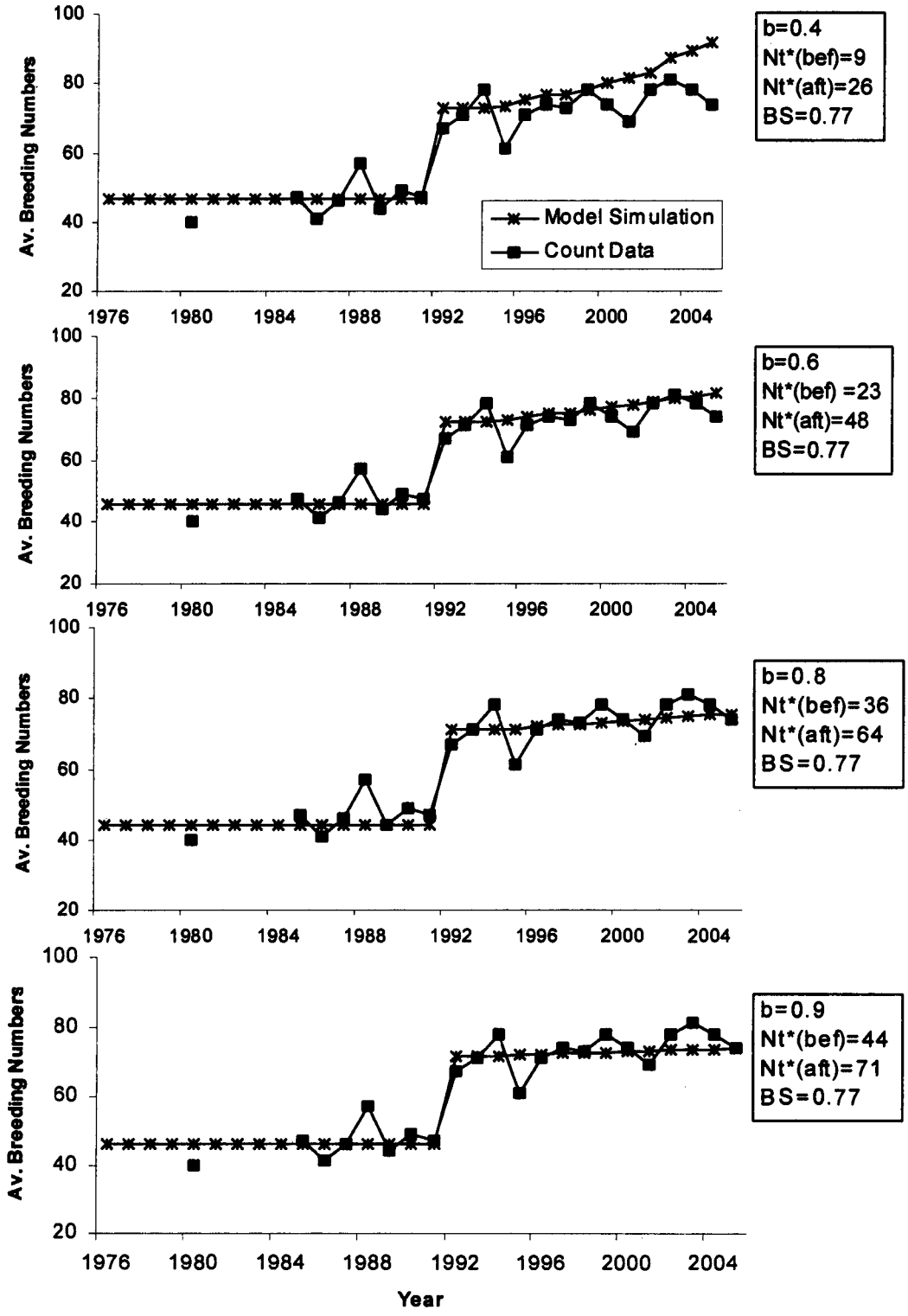

Fig. 7.8. Results of simulations used to attempt to estimate the density-dependent function, *b*, using count data from De Hoop N.R. BS = average breeding success (fledglings.pair^{-1}.year^{-1}), *Nt*'(bef) = the value of *Nt*' needed to fit the model to average breeding numbers before protection, *Nt*'(aft) = the new value of *Nt*', used to fit the model to the average stable breeding population size after it increased and *b* = the strength of the density-dependent function used (low *b*-value reflects strong density dependence and *vice-versa*).

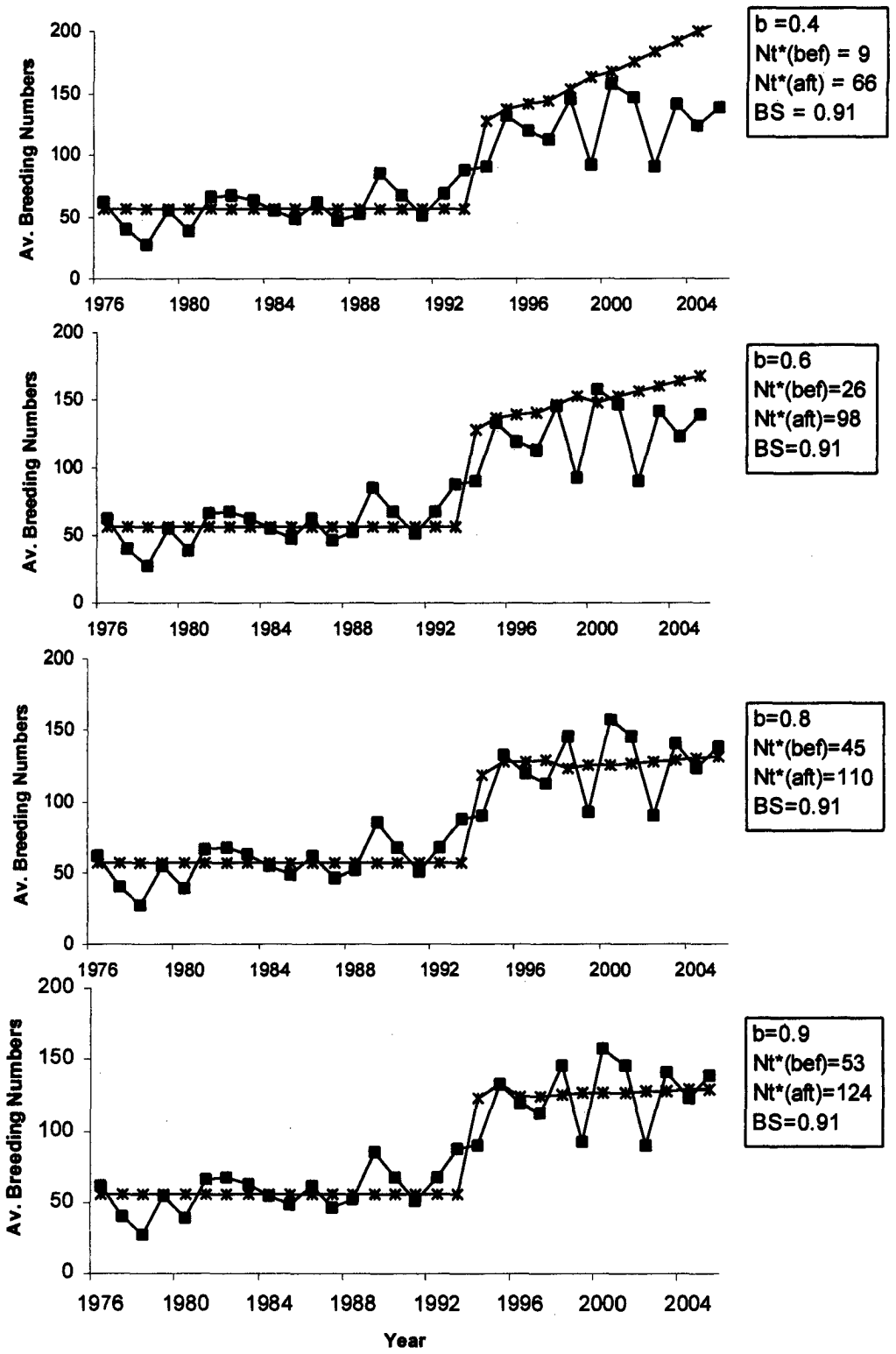

Fig. 7.9. Results of simulations used to attempt to estimate the density-dependent function, *b*, using count data from Malgas Island. BS = average breeding success (fledglings.pair^{-1}.year^{-1}), Nt'(bef) = the value of Nt' needed to fit the model to average breeding numbers before protection, Nt'(aft) = the new value of Nt', used to fit the model to the average stable breeding population size after it increased and *b* = the strength of the density-dependent function used (low *b*-value reflects strong density dependence and *vice-versa*).

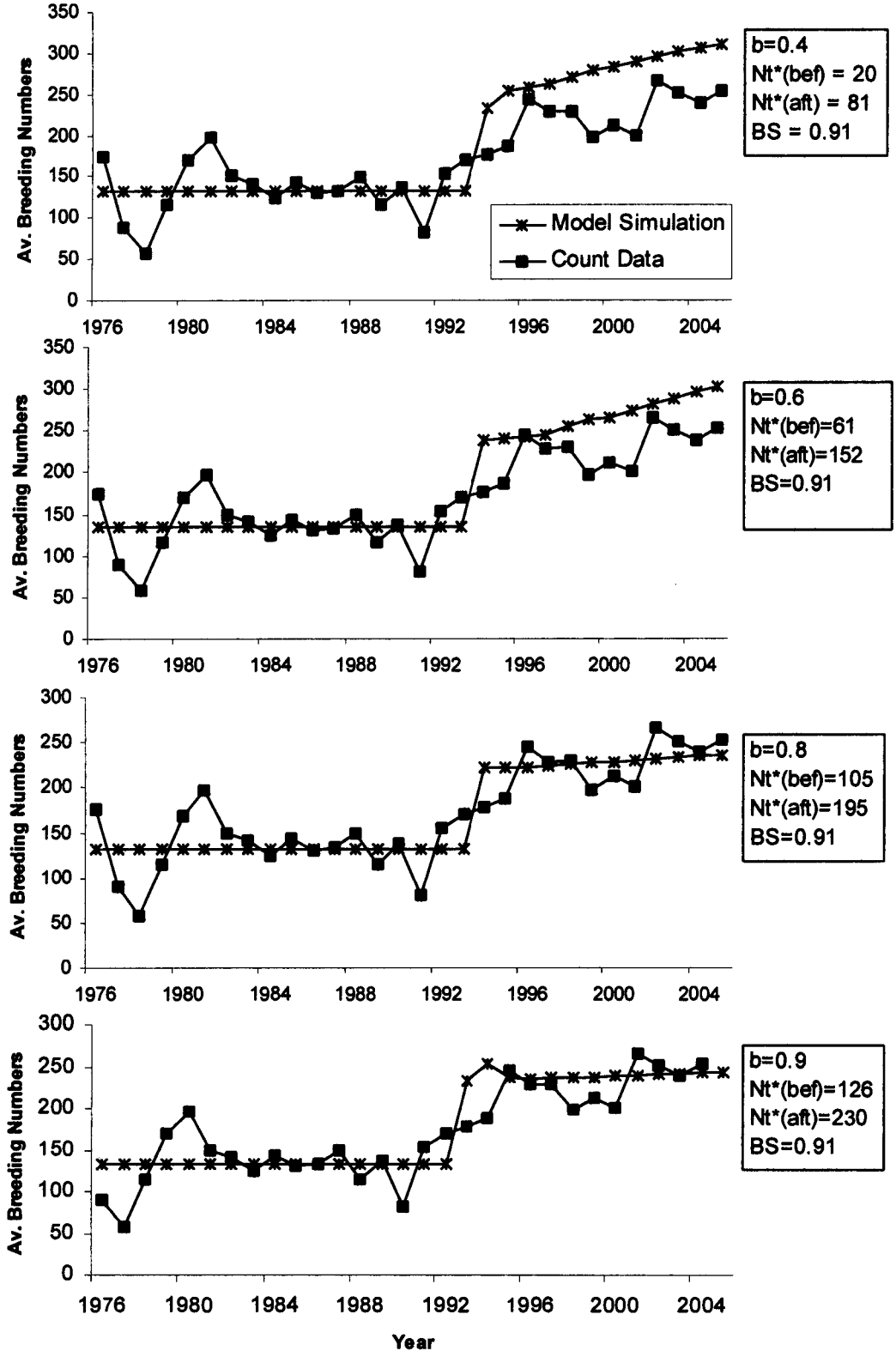

Fig. 7.10. Results of simulations used to attempt to estimate the density-dependent function, *b*, using count data from Jutten Island. BS = average breeding success (fledglings.pair^{-1}.year^{-1}), *Nt*'(bef) = the value of *Nt*' needed to fit the model to average breeding numbers before protection, *Nt*'(aft) = the new value of *Nt*', used to fit the model to the average stable breeding population size after it increased and *b* = the strength of the density-dependent function used (low *b*-value reflects strong density dependence and *vice-versa*).

breeding population will have a relatively large influence on the breeding population when b is small (i.e. the rate at which additional birds can settle as breeders as the total number of birds able to breed increases, is much greater). The relatively rapid, secondary increases in breeding population numbers at low values of b for island populations can therefore be explained by high reproductive rates. Figs. 7.7-7.10 only illustrate the changes in breeding population numbers over the time period for which observational data exist, however, projection of the population forward in time indicates that breeding populations do stabilize as would be predicted by the model, but when b is low, this is at much higher levels than current mean breeding population sizes (see Table 7.1).

The method of estimating the strength of density dependence, based on an hypothesized increase in Nt', assumed that current estimated average fledging success rates persisted over the entire simulation period. However, if breeding success was lower before either food availability or protection improved and only increased to current estimated averages subsequently, this might alter estimates of b. A series of simulations were therefore run where Nt' was manipulated as before, but initial stable breeding populations were established using reduced breeding success (down to 50% of current estimates) and were then increased at the time of improved food supply/protection (as seemed to be the case at Jutten and Malgas Islands – Hockey & van Erkom Schurink 1992). For three sites (De Hoop N.R., and Malgas and Jutten Islands), the results of these simulations indicated that lowering breeding success before protection/food availability improved did not compromise the estimate of b. Interestingly, for Goukamma N.R., initializing the breeding population using average breeding success values of down to half current levels did dramatically alter breeding populations after Nt' was increased, with breeding populations slowly *decreasing* after subsequent rapid increases as a result of increasing Nt'. Reducing b-values speeded up these decreases. These results can be explained by the low reproductive output of birds at Goukamma and the resultant small size of the 'reservoir' of floaters available to settle. At breeding success rates of close to 50% of current estimates, the reservoir of floaters was so small that increasing Nt' to try and attain current breeding population numbers all but depleted the floater population, resulting in insufficient floaters to counter the mortality of breeders. Even more rapid decreases with lower b-values were because of a greater contribution of conspecific pressure in determining breeding population densities. Thus, a low value of b assumes that average territory

size is relatively sensitive to changes in competitor density. Under this scenario, when territorial birds die, adjacent pairs will expand their territories, thus space does not automatically become available. Rather, the floater population must increase substantially before some can intrude successfully and establish territories to replace lost breeders. Given that breeding populations have not decreased at Goukamma over the last 12 years (Table 7.1), it seems unlikely that breeding success of birds was substantially lower at Goukamma N.R. before protection was improved.

Model application

Population projections and local, long-term carrying capacity. Based on uncertainty in the value of *b*, population projections were initially carried out using a range of *b*-values between 0.6 and 1 for each site. However, for De Hoop and Goukamma, using *b*-values higher than 0.9 made no difference to estimates of breeding numbers. Thus, projections for these two sites are based on *b*-values of 0.6 and 0.9. For Malgas and Jutten Islands, the density-dependent effect had little influence on breeding population projections once $b>0.95$. Thus, projections for these two sites are based on *b*-values of 0.6 and 0.95 (Fig. 7.11). For Goukamma N.R., using *b*-values of 0.6 and 0.9 yielded estimates of 47 and 34 (mean value = 40.5) individuals respectively and at De Hoop N.R., the corresponding figures were 95 and 72 (mean value = 83.5) birds. For island populations, absolute differences in projected breeding numbers were greater. For Malgas Island, *b*-values of 0.6 and 0.95 yielded maximum breeding densities of 182 and 132 (mean value =157) individuals respectively. For Jutten Island the corresponding figures were 290 and 233 (mean value = 261.5) breeding individuals. However, more representative estimates, based on proportional changes in numbers between mean values and upper and lower estimates for each site, indicated a similar degree of variation at each site (Goukamma: 16%; De Hoop: 14%; Malgas: 16%; Jutten: 11%). Assuming no regulatory effects on immature and mature non-breeding oystercatchers, it was possible to estimate the maximum stable size of the floater populations generated by local breeding populations at carrying capacity. As expected, floater numbers at Goukamma N.R. were low (lower than estimated breeding populations at carrying capacity) due to the low reproductive success of breeders (Fig 7.11). However, at De Hoop N.R., projected floater numbers were larger than breeding populations at predicted carrying capacities, and at Malgas and Jutten

Islands, predicted floater populations at carrying capacity were more than one and a half times the estimates for breeding population sizes.

Density dependence and stochastic processes. Initial conditions used in stochastic simulation models are outlined in Table 7.2. Statistical comparisons showed that for all sites there were highly significant differences in the mean total population size at 200 years when the strength of density dependence was varied between 0.6 and 1 (Goukamma ($F_{2,2997}$ =1817, p<<0.001), De Hoop ($F_{2,\ 2997}$ = 734, p<<0.01), Malgas ($F_{2,2997}$=657, p<<0.01) and Jutten ($F_{2,2997}$ = 646, p<<0.001)).

Table 7.2: Initial conditions for stochastic model simulations where the density-dependent effect, *b*, was varied between 0.6 and 1 (*b*-values are depicted in bold and, associated Nt' values for each site are given below each of these *b*-values). Initial conditions were established based on the assumption of currently stable breeding numbers (see Table 1) for populations at the four localities. (Note that where b=1, Nt' is the breeding population. When calibrating the model for Goukamma N.R., the same result was obtained with b=0.8, because of the insensitivity of the breeding population to changes in *b* at high values of *b* for this population, as a result of low reproductive rates).

	Breeding Success ($Fl.Pr^{-1}.Yr^{-1}$)	Nt'			**Breeding Population**	**Total Population**
		0.6	**0.8**	**1**		
GK	0.41	27	34	-	34	56
DH	0.77	58	68	-	72	171
MG	0.91	107	123	-	127	324
JU	0.91	195	224	-	232	585

However, the effect of varying density dependence on the mean total population size at 200 years varied substantially at the different localities (see Fig. 7.12). The change in mean total population size when the density-dependent parameter, *b*, was varied between 0.6 and 1, was only 12% for the De Hoop N.R. population, but as high as 75% for the population at Goukamma N.R. At Malgas and Jutten Islands the corresponding differences were also very large (53% and 55% respectively). In all cases, estimates of the mean population size at 200 years decreased as *b* decreased, but the extent of this decrease varied between localities.

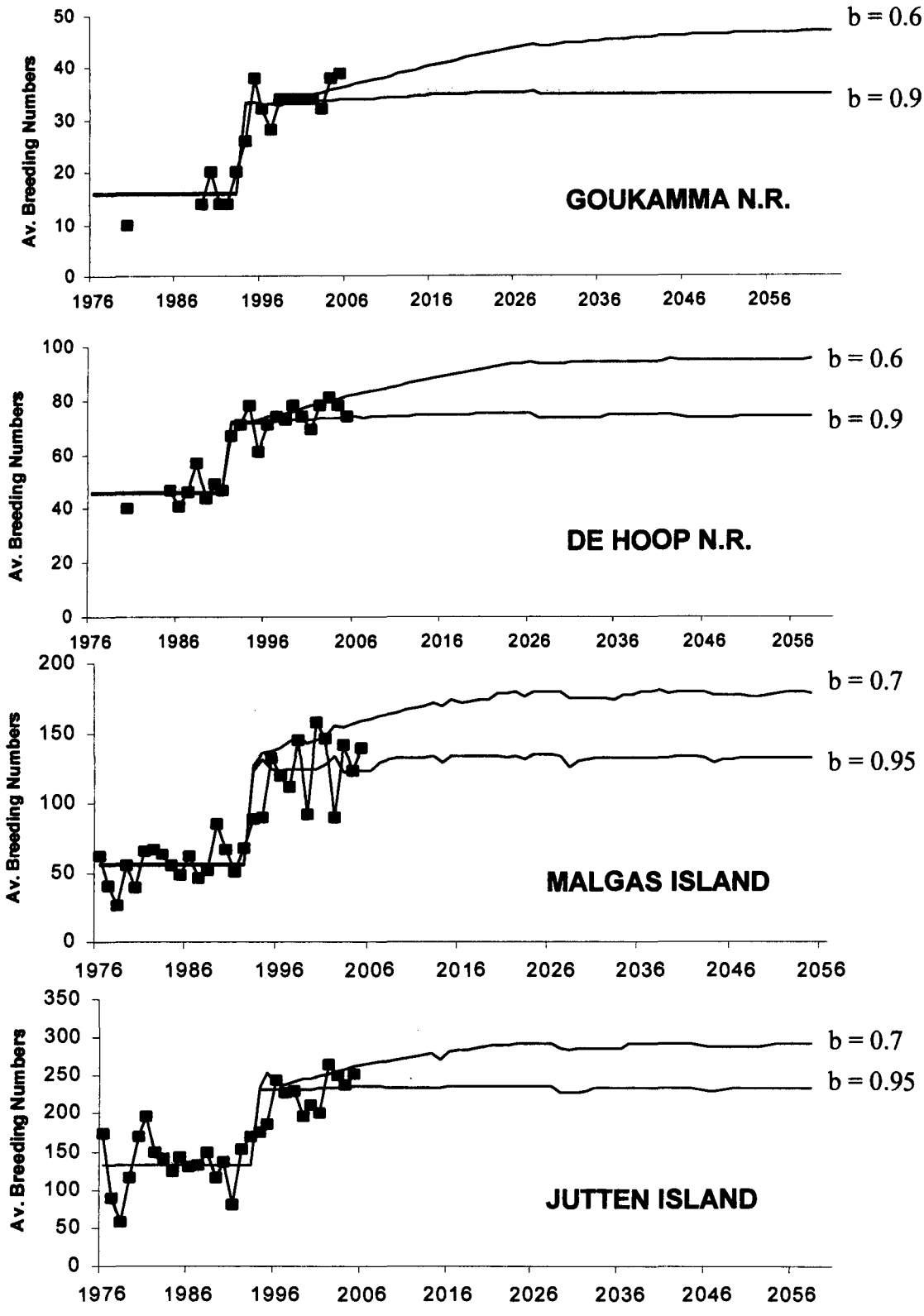

Fig. 7.11: Long-term population projections for estimated breeding numbers at four localities around the coast of South Africa. Projections illustrate the variability in stable upper limits to breeding populations based on uncertainty in the estimation of the density-dependent effect, *b*. Population trajectories simply represent projections of population simulations used to calibrate the model and estimate *b* (Refer to Figs. 7.7-7.10).

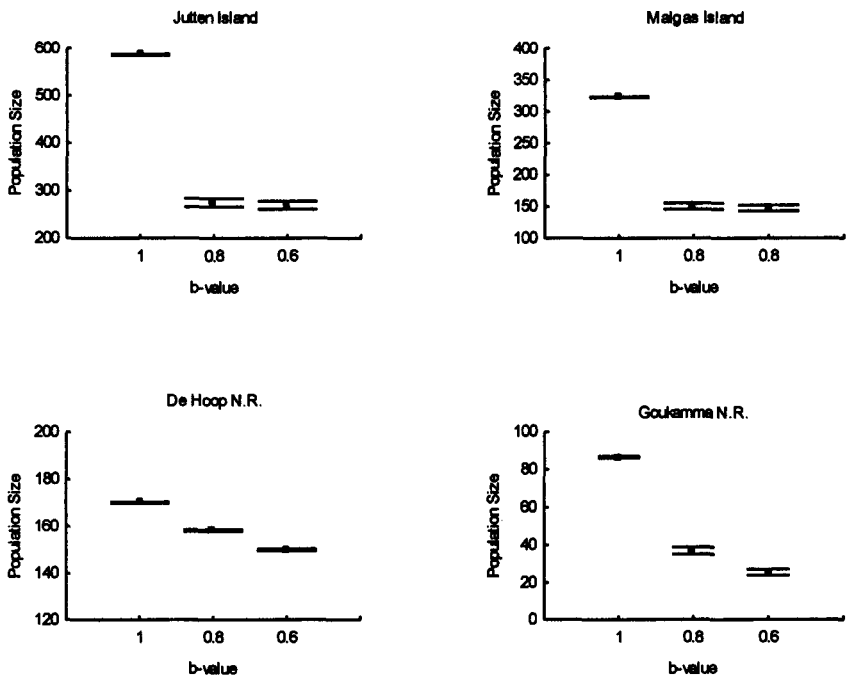

Fig. 7.12: Results of stochastic model simulations for four local populations. Box-and-whisker values represent the mean and S.E. estimates for 200-year runs based on 1000 simulations, for the given level of density dependence (*b*-value). For Goukamma and De Hoop only breeding success was varied, but for populations at Malgas and Jutten, adult mass mortalities were also introduced (refer to the text for details).

At both Malgas and Jutten Islands there were no significant differences in population outcomes when *b* was varied between 0.8 and 0.6 (Malgas: $q_{3,2997} = 0.51$, $p>0.05$; Jutten: $q_{3,2997} = 0.72$, $p>0.05$). However varying *b* between 1 and 0.8 made a large and significant difference to outcomes for populations on both islands (Malgas: $q_{3,2997} = 44.2$, $p<0.01$; Jutten: $q_{3,2997} = 43.68$, $p<0.01$). Population outcomes at De Hoop were significantly different when *b* was varied between 1 and 0.8 ($q_{3,2997} = 31.9$, $p<<0.01$) and when *b* was varied between 0.8 and 0.6 ($q_{3,2997} = 22.1$, $p<<0.01$). For Goukamma, similar results were obtained (b=1 *vs* b=0.8: $q_{3,2997} = 65.1$, $p<<0.01$; b=0.8 *vs* b=0.6: $q_{3,2997} = 15.7$, $p<<0.01$).

Differences in population outcomes with variation in density dependence can essentially be explained by the impact of this variation on the breeding population. Under conditions where b<1, when adult breeders die then vacancies are not immediately filled, even if there are floaters. This is because neighbouring breeders

expand their territories and floaters have to build up sufficient numbers (due to asymmetry in the competitive process) to force their way into the breeding population.

At Goukamma N.R., because mean breeding success is low, floater numbers are generally low, and thus, in years when floater numbers are low, the floaters are unable to establish territories in between existing territory holders. Where b=1 this does not occur, because territory size is assumed to be fixed at a particular resource level and not compressed by conspecific pressure. Thus, if breeding space becomes available, neighbouring pairs do not expand their territories and vacancies can be instantly occupied by floaters, provided there are enough floaters available.

Population outcomes at De Hoop N.R. were not very sensitive to the density-dependent effect, because breeding success is high and thus, even with some fluctuation in floater numbers from year to year (as a result of fluctuating breeding success), floater pressure was sufficient to maintain fairly stable breeding populations from year to year, even when b<1 (Fig. 7.13).

Population outcomes for island simulations were very sensitive to the density-dependent effect primarily because breeding populations were subjected to mass mortalities and hence heavily impacted fairly frequently. At low b-values the breeding population is controlled largely by the size of the floater population, but because of the asymmetric nature of competition between birds holding territories and those excluded, when the breeding population is impacted by a mass mortality, the recovery of the breeding population is very sensitive to the size of the floater population. If the floater population is not large enough to place sufficient pressure on potential breeding space, the breeding population will not recover quickly and thus there is a much greater probability that the breeding population will be impacted by further mass mortalities before it has fully recovered. Under a scenario where b<1, populations are very unstable (Fig. 7.13) and the probability of population crashes are much greater, because the breeding population can be quickly reduced to critically low levels by a series of mass mortalities. For simulations at Malgas and Jutten Islands, there were indeed very large variabilities in the population outcomes and there was a high probability (33-37%) of populations crashing (<5% of initial numbers) when b was between 0.8 and 0.6.

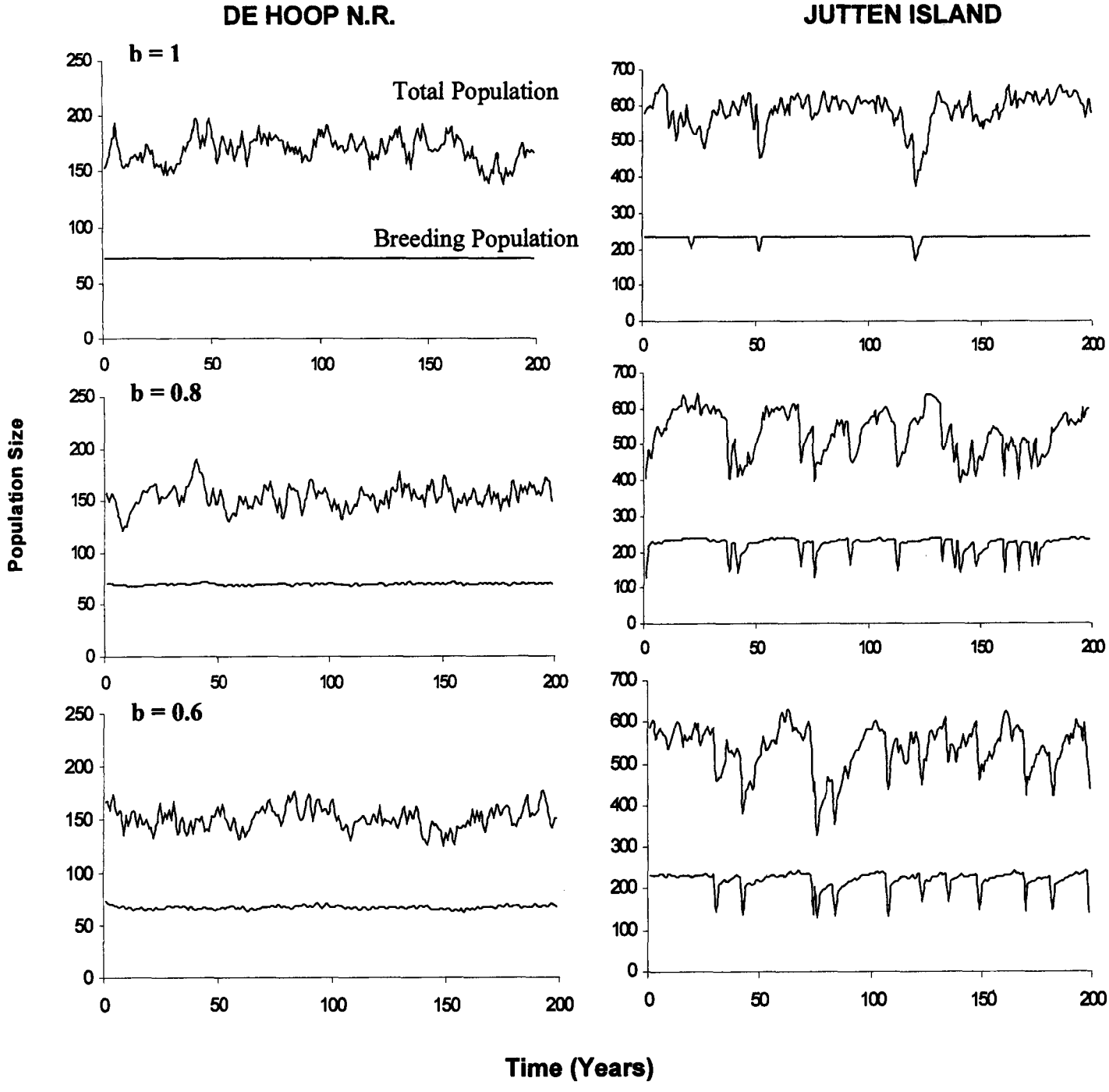

Fig. 7.13: An example of stochastic model simulations for two study populations. Each graph illustrates a 200-year run using the specified density-dependent effect, *b*. In the case of simulations for De Hoop N.R., variability in breeding success (fledglings.pair^{-1}.year^{-1}) did not have a large effect on population predictions when *b* was varied. However, stochastic simulations of the population at Jutten Island indicated that, in the context of a population experiencing mass mortalities (as with the population at Malgas Island), varying the strength of the density-dependent relationship had a very large and variable impact on population outcomes (refer to the text for details).

DISCUSSION

The central argument developed here to explain changes in breeding numbers of oystercatchers at four localities following improvement in habitat quality (either through protection or improved food availability) is based on two hypothesized processes. Firstly, in the face of improved habitat quality, territorial oystercatchers reduce territory size to optimise the cost/benefit ratio of territoriality (Fig. 7.14). As a result, previously excluded, sexually mature birds are able to establish territories in vacancies made available by territory shrinkage. The model interprets this process as an increase in the population threshold (Nt') at which exclusion of sexually mature birds begins, with Nt' essentially reflecting the contribution of habitat quality in determining population densities. An increase in Nt' covers all possible factors (food availability, chick-rearing habitat, nesting habitat etc.) contributing to improved habitat quality. Simplistic as this interpretation of Nt' is, it may be reasonable for African Black Oystercatchers because, unlike the better-studied Eurasian Oystercatcher, breeding adult African Black Oystercatchers are sedentary (Hockey 1996). There is currently little evidence (other than the interpretation of the observed pattern of changes in breeding numbers themselves) to indicate that higher breeding densities are due to either (1) existing territory holders reducing average territory size as a result of improved average habitat quality, allowing previously excluded birds to settle, or (2) increased floater pressure enabling birds to force their way into a territory. However, model simulations strongly suggest that increases cannot be explained by hypothesis (2). Hypothesis (1) appears to be a much more likely explanation based on the favourable comparison between model simulations (i.e.manipulating Nt') and the observed pattern of changes in breeding numbers. One other line of evidence, based on count data, also strengthens Hypothesis (1). Summer count data from Goukamma N.R. indicated that the rapid increase in the number of breeders between 1992 and 1995 was concomitant with a depletion of the non-breeding population adjacent to the breeding grounds (Fig. 5.4). This strongly suggests that, at least at this site, this pool of non-breeders were sexually mature birds, previously excluded, but able to obtain a territory due to shrinkage of existing territories. The increase in the breeding population certainly cannot be explained via annual recruitment of previously immature birds (Ch. 5). A further difficulty with Hypothesis (1) is that it requires a demonstration that reduction in territory size

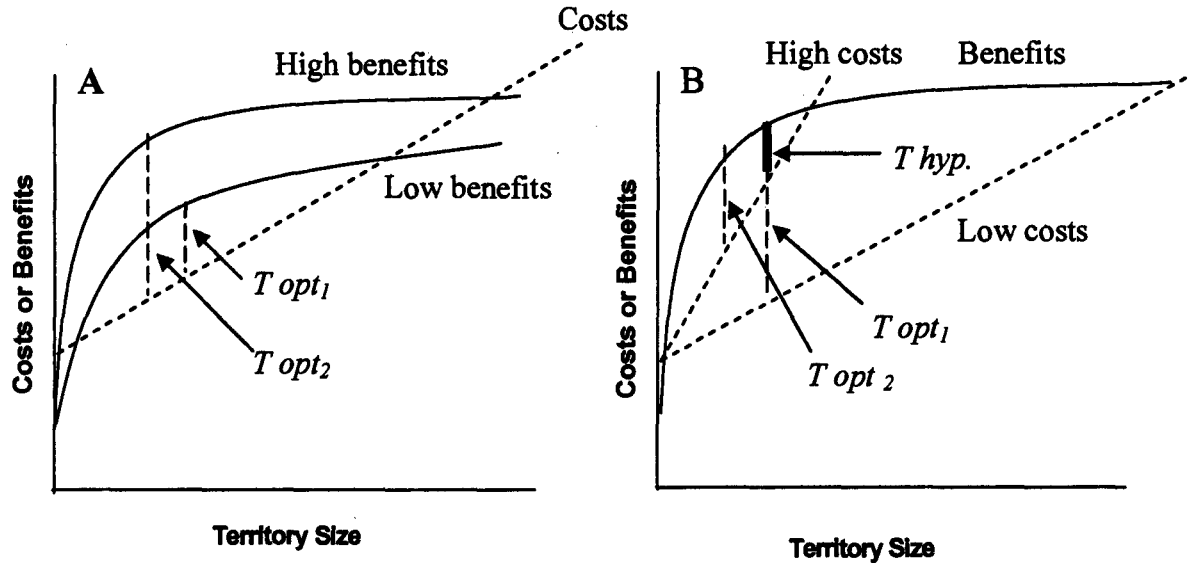

Fig. 7.14: Schematic representation of how reduction in territory size in response to improved food supply as opposed to conspecific pressure is viewed in the model, from the perspective of the territory owner. In (A), reduction in territory size is beneficial when resources improve, because net gains (*T opt*) increase with a decrease in territory size. In (B), territory size is reduced, but not to maximize net gains, because with increasing competitor density, the cost curve increases more rapidly with an increase in territory size. Thus with adequate conspecific pressure, territory holders reduce territory size to optimize the cost/benefit margin ($T\ opt_2$), but at the cost of reduced net gains (cf. $T\ opt_1$). *T hyp*, represents the net gain to the territory owner if territory size were not reduced in the face of a density-dependent increase in costs to territory defence. Because *T hyp* is less than $T\ opt_2$, it pays to reduce territory size to 'make the best of a bad situation' (Figures modified from Both & Visser (2003)). A *b*-value of unity in the competition model (Eq. 7.2, Methods) is viewed as a situation where a change in competitor density has little influence on the gradient of the cost curve for territory holders. Thus territory size and hence the number of territory holders are not influenced by competitor density.

resulted in an improvement in the cost/benefit margin of territory defence for existing territory holders. In the case of Hypothesis (1), decreasing territory size should result in a greater profit margin for territory holders, compared with Hypothesis (2) where decreasing territory size only 'makes the best of a bad situation'. Under Hypothesis (2), there should be resistance to reduction in territory size (Fig. 7.14). Difficulties with the cost/benefit approach to understanding territory size and hence densities of breeding birds, is that it is frequently difficult to quantify the costs incurred and benefits accruing to territory owners (Krebs & Davies 1981). Nevertheless, there are demonstrations that birds do optimize the size of their territories (and resource density

(usually food) has been experimentally manipulated to show that territory size decreased when resource availability was increased artificially (e.g. Gass *et al.* 1976, Carpenter 1987b)). It is suggested here that oystercatchers responded similarly to resource density and that, of the two main determinants of territory size (resource density and competitor density - Carpenter 1987a), resource density is overwhelmingly important.

Whatever the determining factor(s) of territory size is/are, the model assumes that for African Black Oystercatchers, it is always beneficial for birds to defend a territory. However, there are instances when territorial defence may become altogether unprofitable (Gill & Wolf 1975, Carpenter 1987a,b). In the case of African Black Oystercatchers on sandy beaches on the south coast of South Africa, there is some evidence of territory abandonment, probably in response to temporary periods of locally abundant resources. (The main prey item of oystercatchers on sandy beaches is the white mussel *Donax serra*, which is highly mobile). On the sandy beaches east of the Sundays River (33°43'S 25°51'E) on the south coast of South Africa, immature oystercatchers feed in loose flocks near areas of highest food availability, presumably because territorial defence is unprofitable in these areas (Ward 1990). In the same areas, some adults (perhaps most) abandon territoriality in the non-breeding season and often forage in flocks, presumably gathering in areas where *Donax* are temporarily superabundant (P.A.R. Hockey pers. comm.).

One of the puzzling features of the model simulations when compared with observed population sizes from the four localities is the 4-6 year lag between projected increases and the observed increases in estimated breeding numbers. Although the time between improved breeding success and age-at-first breeding is at first a seemingly obvious explanation of this lag, results strongly suggest that improved breeding success alone cannot explain rapid changes in breeding numbers at any of the study sites (e.g. Fig. 7.6). A possible answer to this seeming conundrum lies in the ability (or otherwise) of territorial oystercatchers to adjust territory size to improving environmental conditions. Most studies demonstrating territory adjustment to resource levels have focused on species that defend short–term territories (e.g. Holmes 1970, Cody & Cody 1972, Gill & Wolf 1975). African Black Oystercatchers not only defend territories in the long term, but most also defend their territories year-round. Other studies have shown that species with long-term territorial systems, although displaying varied territory size in different areas and between habitat types,

show no change in territory size in response to short-term changes in food abundance, even when these changes are large (Patterson 1980). Patterson (*op. cit.*) argued that in such species, stability in territory size could well have evolved as an adaptation to long-term stability in 'average' resource levels. Under these conditions, it would be maladaptive to reduce territory size for short-term gain in response to short-term improvement in resources, because the costs of attempting to regain lost territorial ground when resource abundance decreased could well be prohibitive. Given that oystercatchers conform to the criteria of species with long-term territorial systems, (*sensu* Patterson 1980), it is likely that the African Black Oystercatcher has evolved such a system of territory defence. However, this does not preclude adjustment of territory size to track resources, but rather inertia on the part of individuals to do so. Most studies demonstrating that species with long-term territorial systems do not adjust territory size in response to a change in resource levels have allowed for only short response times (e.g. Charles 1972, Hirons 1976, Gill & Wolf 1975, Mares *et al.* 1982, McNair 1987). Although no resource manipulation experiments have been undertaken for African Black Oystercatchers, the invasion of the alien mussel *Mytilus galloprovincialis*, as well as increased protection at the four study localities, have provided a natural experiment allowing some insight into long-term responses of populations to improved habitat quality.

If protective measures as well as food supply have influenced the territory size of oystercatchers, this begs an explanation of how the former may have had this effect. A common benefit for oystercatchers is likely to have been reduced disturbance by humans and their pets, primarily dogs. High disturbance prior to protection may well have artificially increased the total breeding and foraging area defended by resident territorial adults, resulting in a decrease in the profit margin of territorial defence. There is evidence for this from at least one area on the Cape Peninsula, South Africa (Ch. 2), where breeding and feeding territories are now totally disjunct, almost certainly due to ideal breeding habitat backing the feeding grounds becoming too heavily disturbed for birds to breed successfully. The latter scenario has particularly acute and negative implications for the ability of oystercatchers to rear their young (Ch. 4).

Up to this point, the focus of the hypothesis as to how populations have responded to changes in habitat quality has been developed from the perspective of territory owners and how they might respond to both changes in resources and

conspecific pressure. However, there is increasing evidence, at least for oystercatchers (Ens 1995 *et al.* 1995, Heg *et al.* 2000, Bruinzeel & Pol 2004), that floaters are not simply inferior competitors excluded from obtaining breeding opportunities. Rather, nonbreeders actively make decisions with regard to when they should attempt to establish a territory in the face of competition, specifically whether they should attempt to establish a territory early (with possible negative fitness effects as a result of the competitive process) or wait (foregoing some years of breeding and incurring an elevated risk of dying before breeding for the first time). These decisions become more complex when spatial heterogeneity is considered, because potential settlers have the option of settling in a low-quality habitat where competition is less intense, or waiting for an opportunity to settle in a high-quality habitat. Both theoretical and empirical studies of Eurasian Oystercatchers have concluded that as a result of these decisions, queues of potential settlers develop. The act of queuing for a specific territory reduces an individual's chances of settling elsewhere and complex site- and time-dependent dominance hierarchies develop among queuing individuals (Ens 1995 *et al.* 1995, Heg *et al.* 2000, Bruinzeel & Pol 2004). Understanding the decisions that potential settlers must make, both on when and where to settle, is likely to be particularly important in trying to understand changes in local breeding densities in the context of changes in habitat quality (e.g. Kokko & Sutherland 1998). The simple territory shrinkage model advanced here to explain changes in breeding populations at four localities assumes no large spatial variability in habitat suitability within sites (either linked to breeding or feeding habitat) and that, as a result of improvement in habitat quality, potential settlers did not simply decide to settle in areas that were previously unoccupied. This assumption is likely to be reasonable for birds settling on islands, where territories are closely packed. Resources are fairly evenly distributed around the islands, although there are some subtle differences in microhabitat quality for oystercatchers (Hockey 1982). Some pairs on islands have established inland breeding territories over the years. This is clearly not due to existing territory holders reducing their territory size, because inland breeders are spatially disjunct from the breeding population along the shore. However, inland pairs represent a very small proportion of the total population and most commute to feeding territories on the mainland (Ch. 5).(On Jutten Island where there is a clear spatial distinction between inland breeding pairs and the rest of the breeding population, it is estimated that inland breeding pairs comprise less than 5% of the entire breeding population (pers.

obs.).On Malgas Island it is more difficult to decide what defines an inland breeder. However, the proportion of inland breeding pairs is likely to be even smaller since the island is much smaller (and therefore the perimeter to area ratio much greater) and the central area of the island is occupied by a large breeding colony of Cape Gannets (*Morus capensis*) during the summer months). However, habitat suitability at De Hoop, and particularly at Goukamma, is variable and oystercatchers within these study areas are unevenly distributed along the coastline. Is there any evidence to suggest that potential settlers responded to improvement of previously poor quality habitat by favouring areas outside of those occupied by territorial pairs, but within the study areas? Ultimately, without mapping of territory size over time, it is difficult to answer this question definitively. However, at Goukamma N.R., the distribution of territorial pairs over time, in relation to the two habitat types that occur there (mixed and sandy shores, representing good and poor-quality foraging habitat respectively - see Ch. 2 for shore type definition) has been mapped. It could be predicted that if poor quality habitat has become more favourable over time, relative to good quality habitat (as a result of higher population densities on mixed shores) then the ratio of breeding densities on mixed shores relative to that on sandy shores should have decreased over time. However, densities have increased approximately threefold on mixed shores, which represent less than one-third of the entire area (Oystercatcher Conservation Programme unpubl. data). During the same period, only one pair has settled on sandy shore, which make up two thirds of the coastline at Goukamma Nature Reserve. The ratio of breeding densities on mixed shores relative to sandy shores has therefore increased dramatically.

It is important to note that these different interpretations of how increased settlement may have occurred at the four sites does not compromise the hypothesis that increased settlement (as interpreted by a change in Nt'), coupled with a breeding population whose average territory size is relatively unaffected by changes in competitor density (high b-value), explains the changes at these four localities.

By using changes in estimates of breeding populations, it was possible to estimate the strength of density dependence, b, in terms of the possible influence conspecific pressure might have on establishing stable breeding densities. The weakness of this approach is the insensitivity of the breeding population to changes in b when b is high. For b-values higher than approximately 0.6 it was only possible to estimate b to within a range of values between 0.6 and 1, although consideration of

the results from simulations of island populations suggest that *b* exists in a smaller range of values - somewhere between 0.8 and 1 - indicating that competitor density has little influence on territory size (and hence the density of breeding birds).

Consideration of stochastic processes operating in populations with low reproductive output or experiencing mass adult mortalities, showed that the difference between a *b*-value of 0.8 and 1 (the latter situation being one where optimal territory size is not density dependent) on population outcomes is considerable. Despite this uncertainty, however, there is at least one good reason – based on the species' life-history - to suggest that *b* is likely to be much higher than 0.6, and closer to 1, and also that, at least for the African Black Oystercatcher, *b* may well be independent of habitat quality (as assumed in the model). The density-dependent effect is viewed here as a parameter which reflects the competitive asymmetry between territory holders and birds which are excluded, and is likely to be close to 1: floaters have little chance of influencing average territory size and hence influencing breeding density. Furthermore, because territory size is fixed for a given resource level, when vacancies do become available through the death of territorial birds, established neighbouring pairs do not enlarge their territories. Thus, floaters can buffer breeding populations (i.e. fill vacancies), but there is no density-dependent effect. It is speculated here, as suggested for other bird species (Patterson 1980), that African Black Oystercatchers have evolved to defend a relatively inflexible territory size for a given resource base and that this is adaptive in a non-migratory bird which lives in an environment in which resource levels are fairly constant (Hockey 1996). Furthermore, the strength of territory defence and the birds' inflexibility in adjusting territory size may well be a pair of genetic characteristics that cannot be separated from each other. Thus, strength of defence may come at the price of inflexibility if resources vary over the short term. Under these conservative conditions, floaters have little (if any) influence on territory size, but at the same time, if resources vary, oystercatchers cannot adjust territory size immediately to optimize the cost/benefit margin of territory defence. Overall, there is little within-site interannual fluctuation in the standing stock biomass of rocky shore invertebrates in South Africa, and inter-site differences are driven primarily by physiochemical differences (Wieters 2006). Thus, in the long-term, resource levels (at least food) vary little, supporting the contention that African Black Oystercatchers have evolved a system of inflexible territory size. The one exception to this lack of variation in resource levels has arisen

with the invasion of *Mytilus*, which has greatly increased invertebrate biomass on the shore (Robinson *et al.* 2005). It seems reasonable, therefore, that territorial birds that have evolved in a situation of natural resource stability would show (at least short-term) resilience to behavioural change should resource levels change.

If, because of this inflexibility, floaters have little influence on territory size, there is no reason to suggest *a priori* that *b* will vary across habitats, although *Nt'* will: this forms the model's description of the contribution of resource levels to population densities in different habitats. However, empirical evidence from Eurasian Oystercatchers suggests that *b* may differ across different breeding habitats (K.B Briggs unpubl. data, K.-M. Exo unpubl. data, cited by Goss-Custard *et al.* 1996a). If this difference in *b* is real, how can it be explained for Eurasian Oystercatchers in the context of *b* reflecting an evolved system of competitive asymmetry? Eurasian Oystercatchers are fundamentally different from African Black Oystercatchers in that adults are migratory and move between winter feeding grounds and summer breeding grounds (Hockey 1996). Individual Eurasian Oystercatchers are highly site faithful to wintering (Ens and Cayford 1996) and breeding (Hulscher *et al.* 1996) areas and have fairly stable long-term breeding territories (Harris 1970). However, they are forced to change their diet seasonally when they switch habitats and it is highly likely that these dietary changes are more pronounced compared to resident, coastal species, although reliable seasonal data are lacking to test this supposition (Hockey 1996). If migratory races of Eurasian Oystercatcher are highly faithful to nonbreeding and breeding grounds, but have to make large dietary changes on a yearly basis, this may well result in the evolution of a more flexible territory defence behaviour than is the case for the African Black Oystercatcher. This would enable birds to adjust territory size more rapidly in response to short-term changes in resource quality. However, if the strength of territorial defence and the flexibility of defence behaviour are trade-offs, then birds with more flexible defence behaviour are also more vulnerable to having territories compressed by conspecific pressure. Under these conditions, the degree of competitive asymmetry would be weaker and reflect in the model of competitive asymmetry (Eq. 7.1) as a lower *b*-value. The act of migration itself may also play a role by weakening the asymmetric relationship between territory holders and floaters because even previous season's territory holders have to re-establish territories each year when they return to the breeding grounds.

If there is a trade-off between flexibility and strength of territorial defence, and migratory oystercatchers are highly site faithful to nonbreeding and breeding grounds, then it seems possible that different systems, reflected in the strength of competitive asymmetry, may have evolved for different migratory populations, and also for nonmigratory populations. It could be predicted that for migratory populations where individuals experience the least difference in resource variability between wintering grounds and summer grounds, competitive asymmetries in the population would be strongest, and thus conspecific pressure would potentially have the least influence on territory size. This should be reflected by a higher *b*-value.

At least one study of *H. palliatus* (Vines 1979) suggests that competitive asymmetries in breeding territory acquisition may not be habitat specific. In the study, both models and live, tethered oystercatchers were used as 'intruders'. Both models and live birds were shifted fixed distances between the boundary and the middle of territories and the level of aggression of territory holders was quantified at each stage. The procedure was undertaken in two different habitats where territorial oystercatchers occurred at different densities. In the two habitats (where birds were breeding at different densities) the aggressive responses to intruders of territorial birds breeding at high densities were simply upper, truncated versions of the response curves of residents in the habitat where breeding densities were lower. Thus, response curves for birds at high densities (in high-quality habitat) had exactly the same slope and elevation, but represented only the upper portion of the response curves for birds at low densities (in low-quality habitat). Although aggressive response behaviour cannot be directly equated to the degree of exclusion, the *change* in the degree of exclusion with increasing competitor density may well be directly related to a *change* in the level of aggressive behaviour of territory holders as competitor densities increase.

In this study, there was no empirical evidence to support the assumption that *b* is constant across habitats. However, among African Black Oystercatchers, observed changes in population densities in very different habitats, could be adequately simulated by manipulating the population density at which exclusion begins. Based on the results of these model simulations, there is therefore no reason to assume that *b* must differ *between* habitats in order to explain the breeding population changes at the four study sites. The assumption that *b* is a species-specific constant (Eq. 7.2) also precludes the density-dependent relationship itself changing with the total potential

breeding population. This is contrary to a number of studies which incorporate the idea of a minimum fixed territory size for a given habitat into models of population dynamics of territorial species (e.g. Brown 1969, Klomp 1972, 1980, Goss-Custard 1996a, 1996b). In these models, it is asserted that at some point, in a given habitat, no matter how many potential birds are available to establish territories, the number of territories remains constant, and that at this point, the *b*-value is unity (e.g. Klomp 1980, Goss-Custard 1996a, 1996b). The model presented here differs fundamentally in the interpretation of what a *b*-value of unity truly reflects. It is asserted here that in the context of a territorial animal, a *b*-value of unity simply reflects *a system of competitive asymmetry where a change in competitor density has no influence on optimal territory size*. However, *it is not the ultimate endpoint of a process of conspecific compression of territories.* The confusion in the interpretation of *b* is due to the fact that even in the case of *b*-values much less than 1 (i.e. where conspecific pressure has a relatively large influence on the number of territory holders), because of the asymptotic nature of the competitive relationship, the proportion of competitors excluded with an increase in the total number of competitors very nearly approximates a situation where $b=1$ when the total number of competitors is large. This is basic to the concept that the very nature of territoriality itself is a logarithmic form of competitive asymmetry, irrespective of *b*, and is reflected in the fundamental model Eq. 7.1. Thus, the 'one in, one out' rule (Goss-Custard & West 1997) at high population numbers is effectively satisfied for a range of *b*-values when the number of competitors is large. The concept of carrying capacity within the context of a territorial bird must consider the fundamental territorial nature of the animal itself. Certainly for the determination of long-term carrying capacity for the African Black Oystercatcher, it would seem to be more meaningful and more useful to consider equilibrium population size as the only realistic definition of carrying capacity.

It would appear that for African Black Oystercatchers, conspecific pressure has little influence on breeding densities. Thus, the density-dependent effect of conspecific pressure, as a process which works counter to population regulation, appears unimportant. Population regulation is thus likely to occur through breeders adjusting territory size in response to resource availability, with changes in conspecific densities having little influence and floaters only being able to enter the breeding population when vacancies become available. This leads to relatively strong population regulation because the net *per capita* growth rate of the population

decreases as the floater population increases. Floaters therefore buffer breeding population decreases by replacing breeders that have died and also buffer population size because as they accumulate the *per capita* growth rate of the overall population decreases.

Despite the persistence in the notion of b=1 reflecting an endpoint in the process of territory compression, there appears to be no convincing support for this. For example, in his model of density-dependent territory size, Klomp (1980) simply assumed that the maximum observed densities of breeding Great Tits *Parus major* reflected a scenario where b=1, the end-point of a territorial compression process. However, very high densities could have been achieved simply through territory shrinkage in response to high resource availability as is hypothesized to be the case for African Black Oystercatchers (see Fig. 7.14A). In fact, this is much more likely, because very few floaters were observed, even at these high breeding densities. Because of the fundamental competitive asymmetry between floaters and territory holders, it can be predicted that if floaters were influencing territory size, there would have to be very large numbers present in order to lead to such high breeding densities.

The model used in this study assumes a logarithmic relationship between the proportion of competitors for space and the total number of competitors (Eq. 7.2). Thus it cannot be used to validate the assumption that b is a constant, independent of density. A behaviour-based model of Eurasian Oystercatcher population dynamics made no *a priori* assumptions with regard to the density-dependent function as competitor densities increased. Rather, it was allowed to develop based on the behaviour of individual birds (Goss-Custard *et al.* 1996b).

It is important to point out that the latter model describes birds competing for food on the nonbreeding grounds. Nevertheless, if territoriality is operating and can be described by Eq. 7.1, then a constant density-dependent function should be expected. In the case of birds competing for breeding territories 'losers' can be thought of as birds excluded from prime breeding territories, while in the case of birds competing for prime feeding habitat 'losers' are birds forced to move to lower quality habitats or birds that die. The consequences of exclusion are important in population dynamics, but are secondary to the pattern of the exclusion process itself. In this same study (Goss-Custard *et al.* 1996b), it was remarkable that, whichever set of assumptions (regarding individual behaviour of competitors) were used (in each case giving rise to a b-value of <1), it proved impossible to force the density-dependent function, b, to

change from a value <1 to 1, even when entirely unrealistic productivity rates (eight times the observed rates) were applied and in the most favourable of circumstances giving rise to very high densities of competitors. Furthermore, in the same simulations, a number of curvilinear functions were generated, based on different assumptions of the mortality function. However, for each of these scenarios it appears that the *b*-value did not change, regardless of competitor density. In these simulations, it appears that the populations always reached equilibrium without the *b*-value changing and well below the carrying capacity predicted by *b*=1 (Goss-Custard 1996b). Given that these results are based on an individual game theory approach (Maynard Smith 1982) to modeling population dynamics, it likely that they are fundamental. Further, they strongly suggest that interference competition (ultimately leading to increased mortality) as opposed to exploitation competition is overwhelmingly important in governing population dynamics (Goss-Custard *et al.* 1996b). This has indeed been demonstrated using models of foraging behaviour (Goss-Custard *et al.* 2001). However, even more than this, the fact that the results of these behavioural models indicate that the density-dependent function, *b*, does not change with density, suggests that a constant *b*-value, reflecting a density-dependent function independent of competitor density, may be fundamental to and descriptive of the population dynamics of territorial systems.

Simulation models of metapopulation dynamics of Eurasian Oystercatchers have shown that the carrying capacity (as defined by *b*=1) could be reached locally on wintering grounds over one season if disproportionate numbers of birds moved to a few local sites. However, surely the more logical explanation is that this reflects a situation where territoriality no longer operates? It is suggested here that, in the context of a territorial animal, the interpretation of carrying capacity as a situation that occurs when *b* changes from a value of <1 to a value of 1 is fundamentally incorrect. The reason for this is that because the very nature of territoriality itself, as a form of highly asymmetric competition, means that the modelling of territorial systems must be reflected by a situation where no matter how strong the influence of the number of breeders that are able to breed (very low *b*-value), is on the number that do breed there is *always* the *potential* for more birds to establish territories in areas where territorial birds already exist (i.e. *b* is *always* less than one).. In reality, however, when breeding densities are high, the extra number of potential breeders required to cause even a small further increase in the breeding population, is very large indeed (and unrealistic

in nature). This is reflected in the asymptotic nature of the relationship (at high densities) between the increase in the proportion of birds excluded from breeding and the increase in the total potential breeding population (Fig. 7.1). [Note: In this study, results suggest that for African Black Oystercatchers, the strength of the density-dependent relationship (*b*-value) is probably close to unity. However, in the context of how a *b*-value of unity is interpreted here, *b* is highly unlikely to ever actually be *equal* to unity. If *b* were ever equal to unity, this would mean that an increase in the density of competitors has no influence at all on the density of breeders].

There is good evidence that territorial systems do collapse where either local food abundance is so great that there is very little extra benefit to be gained by defending a territory, or where competitors become so locally abundant that territory holders are overwhelmed (Carpenter 1987b). The latter situation may well be reflected (if rarely) in local overwintering populations of Eurasian Oystercatchers (Goss-Custard *et. al* 1996b). However, these situations, if they occur, reflect a change in individual behaviour at high densities, *not the endpoint of a territorial compression process*. Under these circumstances, it becomes very difficult to see how carrying capacity could be defined, but it seems clear that even in a theoretical context it cannot be defined as the point at which the density-dependent function reaches unity.

Among the Haematopodidae, territorial collapse is unlikely given the low demographic rates for the family as a whole (Hockey 1996) and the model developed in this study cannot account for such fundamental changes in animal behaviour. However, such behaviours appear to be rare and localized (Carpenter 1987b) and are unlikely to compromise large-scale population predictions.

It is suggested here that territoriality, where it occurs, can be defined as a form of highly asymmetric contest competition where, under conditions of increasing population numbers, the proportion of 'losers' will always increase logarithmically with the total number of competitors (floaters and breeders). Thus, at least for oystercatchers, this definition of territoriality considers populations as being evolutionarily 'locked' into a form of competition that is undercompensating (i.e. $b<1$ - the number of 'winners' can always potentially increase, with an increase in the number of competitors, irrespective of the population density). Furthermore, the definition precludes *b* changing with competitor density (i.e. the *k*-value for the proportion of 'losers' during the competitive process only varies linearly with the

logarithm of the density of competitors) at a particular point in evolutionary space or time.

In the context of the definition used here, when b=0 competition cannot be defined because populations have not reached the threshold at which exclusion begins. This definition is based only on the observations and simulations of oystercatcher populations. However, it may prove useful for other territorial systems, although the data necessary to estimate b in practice are likely to be hard won.

The suggestion that territoriality may be generally characterized as a logarithmic form of competitive asymmetry and that particular b-values may reflect evolved systems of territoriality within this broader definition, might aid future insights into the conditions under which territoriality evolved.

Although this definition of territoriality requires that b always be less than one and be fixed as a constant at a particular point in evolutionary space and time, this does not preclude the existence of a wide range of evolved territorial systems (reflected by a wide range of b-values either between species or between genetically distinct populations within a species. Two of these systems have been discussed with reference to two oystercatcher species differing fundamentally in at least one life-history feature (migratory *vs* nonmigratory behaviour). Territoriality has been defined in words as "...a form of asymmetric intraspecific competition....[which] occurs when there is active interference between individuals, such that a more or less exclusive area, the territory, is defended against intruders by a recognizable pattern of behaviour..." (Begon *et al.* 1996). However, a much deeper understanding of territorial behaviour is beginning to emerge with the realization that "...territories are not fixed parcels of real estate. Instead, territories are the fluid outcome of behavioural interactions that determine where individuals settle and how long they stay....." (Gordon 1997). With this growing realization, understanding population consequences of competitive asymmetries (including territoriality) in terms of the population outcomes they produce may prove useful in understanding the conditions under which they evolved.

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CHAPTER 8

CONCLUSIONS

AIMS OF THE STUDY

At the beginning of this study, a number of central aims were identified, which were considered to be of relevance to the conservation of the African Black Oystercatcher. These were to:

1. Reassess the global African Black Oystercatcher population and where changes have occurred to assess the reasons for these changes, with particular focus on the possible importance of the invasive mussel *Mytilus galloprovincialis*, as well as protection status for the species' conservation status (Chapter 2).

2. Assess the relative importance of *Mytilus galloprovincialis* and protection status on the breeding success of oystercatchers and to investigate how and to what extent human disturbance may be acting to influence the breeding success of local populations (Chapter 3).

3. Investigate the possibility of chick starvation as a potentially important form of human-induced mortality and assess whether the presence of the invasive mussel *Mytilus galloprovincialis* may be an important factor reducing this possibility (Chapter 4).

4. Assess levels of natal site philopatry and adult site fidelity for the species and investigate what factors influence the pattern of recruitment of birds into the breeding population (Chapter 5).

5. Assess the population viability of the species with key regard to variability in breeding success, variability of adult mortality rates (particularly mass mortalities), recruitment patterns of non-breeding birds into the breeding population, and connectivity between populations (Chapter 6).

6. Investigate how the species' population dynamics are affected by the interaction between territorial breeding birds and nonbreeding birds, with key regard to how this might influence the response of local populations to changes in habitat quality, local population viability and the long-term carrying capacity of local breeding populations (Chapter 7).

FINDINGS OF THE STUDY

Population changes and the global population size

Comparisons of recent population surveys with historical surveys demonstrate that since the early 1980s, the global population size of African Black Oystercatchers has increased by *ca* 46% and now stands at approximately 6670 birds (Ch.2). At a regional scale, on rocky and mixed shores (as defined in Ch. 2), the evidence from this study strongly suggests that the alien invasive mussel *Mytilus galloprovincialis* has been a major driving force behind population increases in these habitats. Three main lines of evidence support this conclusion. Firstly, a previous study demonstrated a link between the proportion of *Mytilus* in the diet of oystercatchers, their productivity and their population size. The findings from this study, based on ongoing monitoring, further support this conclusion. Secondly, comparisons of long-term oystercatcher population trends on stretches of coast defined by the presence or absence of *Mytilus*, demonstrated a link between *Mytilus* status and the rate of population increases in these coastal areas, although the study was partly confounded by site-specific effects. Thirdly, the increase in oystercatcher population numbers appears to be a widespread phenomenon. On 142 of 163 stretches of rocky and mixed habitat where recent oystercatcher numbers were compared with historical counts, numbers have increased, suggesting a widespread cause for these population changes. (Ch. 2). *Mytilus* is both widespread and well established over almost the entire oystercatcher breeding range, and is the dominant bivalve on the west coast of South Africa. While the presence or absence of *Mytilus* partially explains widespread

population increases, protection of coastal areas has also been an important factor. The evidence from this study suggests that increases in oystercatcher numbers on sandy shores (where *Mytilus* does not occur) is explained by the 'release' of populations from high levels of human disturbance in sandy habitats with traditionally high food abundance. On rocky shores where *Mytilus* is prolific, the findings from this study indicate that protection has also had an additional benefit. Population increases in areas with *Mytilus*, but also with a high protection status have been the most rapid, while in areas lacking both *Mytilus* and protection, populations have experienced insignificant increases in numbers, or remained stable. Populations in areas with either *Mytilus* or protection (but not both) have experienced increases intermediate between those where both *Mytilus* and protection are either present or absent. Again, these conclusion were partly confounded by exceptions to the predicted pattern: however, these exceptions could be explained by site-specific effects. Despite widespread increases in population numbers, at 39 out of a total of 241 study sites, oystercatcher populations have decreased. Although the breeding success of oystercatchers at many sites on the mainland of South Africa is likely to be below sustainable levels (Ch.6), the evidence from this study suggests that most observed local population decreases are more likely due to small-scale movement of birds out of coastal areas where the habitat has been substantially modified by human action. The reasons for this are twofold. Firstly, at nearly all sites immediately adjacent to those where population decreases occurred, there have been rapid increases in population numbers. Secondly, although comparisons of recent survey data with historical survey data span a period of 20-25 years, the longevity of adult birds (found in this study to be 30+ years -Ch. 5) could possibly mask the potential population-level impact of unsustainable reproductive rates over this time period (Ch.6).

Factors Influencing the Breeding Success of Oystercatchers

Despite widespread variation in breeding success of oystercatchers, both spatially and temporally, the breeding success of oystercatchers (mean number of fledglings.pair^{-1}.year^{-1}) differed in three population categories defined by varying levels of human disturbance, namely island populations, protected mainland populations and unprotected mainland populations (Ch.3). While the mean fledging success of populations in the three categories were all greater than those required to at least

maintain stable population numbers, variation in breeding success from site to site suggests that in unprotected areas, some populations have reproductive rates which have resulted in negative intrinsic local population growth rates (Ch. 6). Although differences in breeding success between island populations and protected mainland populations were likely due also to other factors, particularly predation, there was also a difference in breeding success between unprotected and protected mainland populations experiencing equivalent predation levels (Ch. 3). An attempt was made to assess the potential importance of both *Mytilus galloprovincialis* (as an agent which has increased the food supply for breeding oystercatchers) and improved protection (as an agent which has reduced the potentially harmful effects of human disturbance) on the breeding success of oystercatchers. The results from this analysis indicated that protection did not benefit oystercatchers in areas where *Mytilus* was absent, but did improve breeding success of oystercatchers in areas where *Mytilus* was present. Habitat quality for oystercatchers (both for breeding and feeding) varies greatly over relatively small scales, and the degree of protection afforded to breeding birds varies between areas defined as protected in this study. Nonetheless, the results of this analysis suggest that breeding success may only have increased in habitats of very high quality (as defined by high biomass of *Mytilus galloprovincialis*), and where populations have been 'released' from high levels of human disturbance (Ch. 3). In unprotected mainland areas, the most important way in which human activity is impacting on the breeding success of local populations is through predation of small oystercatcher chicks by uncontrolled dogs, and through young chicks drowning, probably as a result of hiding for extended periods (in response to human presence) and being inundated by rising tides.

Chick starvation as a source of human-induced mortality

Several *a priori* reasons suggested that oystercatcher chicks may be particularly vulnerable to starvation as a form of human-induced mortality (Ch. 4). However, three major lines of evidence from this study suggests that starvation is unlikely to be an important factor reducing breeding success in areas where human disturbance is high. Firstly, based on an extensive nest-monitoring data set (Ch.3), the majority of chicks die when they were very young and when their energetic demands are minimal. Secondly, using indices of body condition, the body condition of chicks in areas of high and low human disturbance and between chicks known to have fledged and those

known to have died before fledging, do not differ. In general, visible evidence of poor body condition in African Black Oystercatchers appears to be rare: >1500 oystercatcher chicks have been ringed since 1997 and very few of these showed obvious signs of poor condition (Ch. 4). Thirdly, model simulations linking parental foraging time to chick growth illustrate that even in areas of relatively low intertidal productivity, as much as *ca* 30% of the total time available for adults to forage would have to be lost on a continual basis before the probability of starvation increases significantly. This study was unable to demonstrate whether or not the presence of *Mytilus* (as an agent improving the food supply for parental birds) may have improved the chick-rearing ability of adult oystercatchers (as indicated by an improved body condition of oystercatcher chicks) (Ch. 4). Interestingly, the average body condition of chicks was worse after the *Mytilus* invasion than previously, but this result is quite likely confounded by a density-dependent effect specific to a few islands off the west coast of South Africa (Ch. 2)(data for comparisons of chick body condition before and after the *Mytilus* invasion were restricted to chicks reared on these islands – Ch. 4).

Adult Site Fidelity and Natal Philopatry

It was previously suggested that breeding populations of African Black Oystercatchers on offshore islands might be an important source population for mainland populations which have much lower (and in some cases unsustainable) reproductive rates. However, evidence from this study, focusing on some key breeding populations on islands off the west coast of South Africa, suggests that permanent movement of either breeding adults or chicks reared on islands, is extremely rare, with levels of adult site fidelity and natal philopatry being close to 100% (Ch. 5). Offshore islands represent very high-quality habitats with very high densities of breeding birds and it is clear from this study that sexually mature oystercatchers may wait many years to gain a breeding territory on an island rather than establish themselves in low-quality habitat on the mainland. Although this study was limited by the number of years of observational data, nonbreeding birds of seven years old were observed and it is likely that there may be nonbreeding birds substantially older than this (Ch. 5). Breeding populations on islands have increased over the past 20+ years, but now appear to be stable and very close to carrying capacity, given current conditions (Ch. 7). Evidence from population models (Ch. 6) suggests that this system of exclusive natal island philopatry is likely to be stable and

remain unchanged at carrying capacity. Thus, island-reared birds are unlikely to ever become source populations for oystercatcher populations on the mainland. This study demonstrated a clear, age-based recruitment pattern of oystercatchers into island breeding populations, with the probability of establishing a territory being strongly linked to age (Ch. 5). However, based on very limited data, it seems that it is not age *per se* but rather time spent at a site that is likely to determine a bird's success in establishing a territory in high-quality habitat (i.e. on islands). A similar pattern has been demonstrated for the much more thoroughly studied Eurasian Oystercatcher. Observations of nonbreeding, sexually mature birds show that they are preferentially faithful to mainland roosts adjacent to natal islands. It appears that they use these roosting areas as staging grounds from which to make forays to the islands and they may spend many years shuttling back and forth between natal islands and mainland roosts, presumably in an attempt to establish a territory (Ch. 5). While data from mainland populations is much more sparse, high levels of natal philoptary and adult site fidelity, at a scale of tens of kilometres, are also apparent. At a scale of tens of kilometres, the limited data from this study suggest that mainland populations producing surplus birds are (at least currently) not important sources for ailing populations elsewhere.

Intrinsic Growth Rates and Population Viability

Based on a matrix projection model, the critical fledging success required by African Black Oystercatchers to produce an intrinsically sustainable population is estimated to be 0.28 fledglings.pair^{-1}.year^{-1} (Ch. 6). For three different categories of populations, namely island populations, unprotected mainland populations and protected mainland populations, mean fledging success was found to be higher than this (Ch. 3). However, it is clear from this study that fledging success of African Black Oystercatchers varies substantially, both temporally and spatially (Ch. 3) and incorporating this variability into matrix projections models indicated that at many unprotected coastal sites, there is a strong potential for negative population growth (Ch. 6). As expected for a species which is long-lived, matures late and lays few eggs, intrinsic population growth rates were much more sensitive to adult survival than to fecundity. However, despite the higher sensitivity of the intrinsic population growth rate to variation in adult survival, the real variation in fledging success (both annually and between sites) is so large that it has an overriding impact on estimates of intrinsic

population growth rates and therefore warranted incorporation into population viability analyses (which included stochastic processes). Intrinsic population growth rates are also sensitive to variation in the age-at-first breeding. From a conservation perspective, this warrants further investigation into the pattern of recruitment of pre-breeding oystercatchers into the breeding population. Results from stochastic population models (incorporating variability in breeding success and episodic mass mortalities), suggest that for both mainland and island populations, episodic events of the frequency and magnitude that are documented would certainly not be sufficient to precipitate a global population extinction, or the extinction of smaller, but nevertheless geographically widespread, segments of the global population. (Ch. 6). Models presented here considered unified, single populations for unprotected mainland areas (UMPs), protected mainland areas (PMPs) and islands (IPs), based on differences in mean reproductive rates (Ch. 3). While increased connectivity between these defined populations did improve the viability of the global population as a whole, persistence probability of individual populations treated in isolation was still high (even for unprotected mainland populations which have the lowest and most variable breeding success) (Ch. 6). While single, unified populations, for each of IPs, PMPs and UMPs were assumed in these analyses, in reality PMPs are nested within a matrix of UMPs, while IPs comprise numerous, smaller (and spatially disjunct) island populations. This study has shown that oystercatchers display extremely high levels of natal philopatry, to the point where juveniles return almost exclusively to their natal islands, while on the mainland natal philopatry appears to be high at a scale of tens of kilometres (Ch. 5). Given that severe episodic mass mortalities, such as Paralytic Shellfish Poisoning (PSP), or avian cholera, are known to occur at a local scale, these may precipitate local extinction, particularly of local mainland populations. Increased coastal development has resulted in population decreases at numerous sites on the mainland of South Africa (Ch. 2). While these decreases more than likely often simply reflect movement of birds to other areas of more suitable habitat, the long-term effect of increased coastal development fracturing the mainland population into more numerous and more isolated fragments may be of much greater future concern.

The influence of territorial behaviour on population changes, viability and long term carrying capacity of local breeding populations

While demographic rates (such as fledging success, and first-year and adult survival) are important in assessing the growth potential of populations (Ch. 6), translating growth potential into actual changes in numbers requires an understanding of the factor(s) which may limit such growth. Findings from this study suggest that breeding population size of African Black Oystercatchers is tightly controlled by the territorial exclusion of nonbreeding, sexually mature birds. Unlike Eurasian Oystercatchers, where the total potential breeding population may influence the number of birds that do breed, this density-dependent effect appears to be very weak among African Black Oystercatcher populations (Ch. 7). The reasons for this may be that, unlike Eurasian Oystercatchers which are migratory, adult breeding African Black Oystercatchers are sedentary and generally defend their territories year-round. In the case of populations that are tightly regulated by territoriality, there is usually little real change in breeding numbers from year to year unless environmental conditions change: this certainly seems to be the case amongst African Black Oystercatchers. In this study, at four localities where habitat quality did improve (due to improved protection and an increased food supply), the pattern of increase of local breeding populations were likely due to a reduction in territory size of existing territory holders, and subsequent increased settlement of previously excluded sexually mature birds, rather than through improved breeding success (Ch. 7). At all four of these localities, the long-term carrying capacity of the breeding population is thus closely linked to resource quality rather than competitor density. This situation is likely to be similar for other African Black Oystercatcher breeding populations (other than those in this study) in high-quality habitats, where, under conditions of unchanged habitat quality, potential breeders can only replace existing territory holders if they die. Varying the strength of the density-dependent effect (i.e. the effect of the potential number of breeders on the breeding population) over a fairly small range of values (based on uncertainty in the estimation of this parameter) did have a large impact on the viability of local populations. However, although there was uncertainty in the estimate of the strength of this density-dependent relationship, other lines of evidence suggest that it is very weak (or close to zero) and not likely to vary substantially for African Black Oystercatchers.